LIFE-HISTORY EVOLUTION AND COOPERATIVE BREEDING IN THE SOCIABLE WEAVER

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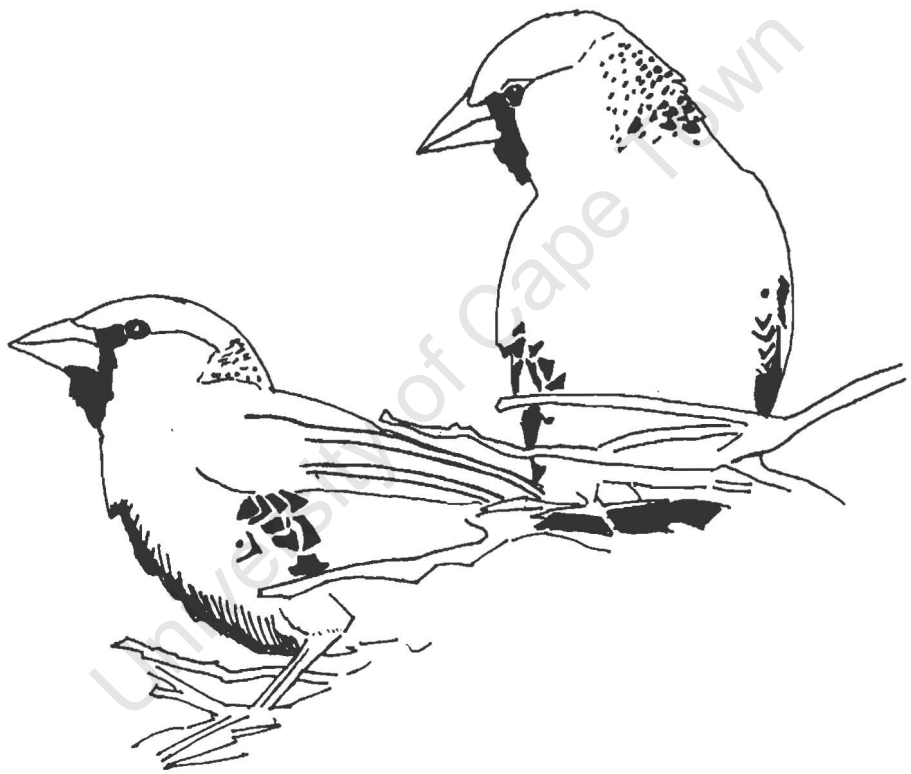

THESIS PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
IN THE PERCY FITZPATRICK INSTITUTE, DEPARTMENT OF ZOOLOGY,
UNIVERSITY OF CAPE TOWN

June 2002

DECLARATION

This thesis describes original research undertaken towards a Ph.D. degree at the Percy FitzPatrick Institute, University of Cape Town, which has not been submitted in any form towards a degree at any other university. I submit it as my own work and have acknowledged all assistance I received in achieving this end.

Rita Covas Monteiro

CITATION

Covas, R. (2002) *Life-history Evolution and Cooperative Breeding in the Sociable Weaver.* Ph.D. Thesis. Percy Fitzpatrick Institute - University of Cape Town, Cape Town.

The sociable weaver nest mass. The photo shows part of colony 2, the largest colony in the study area that during the study period held 150-200 birds. The open savannah habitat characteristic of the area can be seen in the background.

Abstract

When compared to northern temperate counterparts, birds in the tropics and Southern Hemisphere regions, are characterised by low fecundity, long developmental periods and high survival. This pattern has been attributed to hypotheses relating to food limitation, nest predation, and reduced seasonality leading to high adult survival. Still, to date few studies have investigated this issue. In particular, detailed studies from southern regions are scarce and as a result our understanding of this question remains weak. Another characteristic of 'southern' birds is a higher frequency of cooperatively-breeding species. It has previously been shown that cooperative breeding is most frequent amongst species with high survival and low fecundity. An explanation for this could be that long occupancy of territories by long-lived breeders leads to reduced opportunities of independent breeding by young birds. However, the biology of some species is such, that they do not experience shortage of breeding territories or other constraints, while still showing delayed dispersal and cooperative breeding.

This study investigates what factors drive life-history evolution in a cooperatively-breeding southern African passerine, the sociable weaver *Philetairus socius*. This species departs from the traditional cooperative breeding model in being a non-territorial colonial nester that inhabits an unpredictable semi-arid environment. Sociable weavers face no obvious constraints on independent reproduction, yet cooperative breeding is common. Therefore, I also aimed at determining what factors prompt delayed reproduction in this species, since this life history trait is the first step leading to cooperative breeding.

I conducted a field study over three breeding seasons which showed that sociable weavers are typical of 'southern' birds in laying relatively small clutches, having long developmental periods, extended parental care and extended breeding seasons. Nest predation was the main determinant of nesting failure, with an average 70% of clutches laid being depredated. Variation in food availability during the breeding season explained most of the variation in reproductive effort in this species and also influenced reproductive success. However, contrary to what is commonly accepted, it does not seem that variation in food levels during breeding can explain other life history traits of sociable weavers such as high survival. Capture-recapture over eight years showed that sociable weavers enjoy relatively high survival (0.66 annual survival rate). Unlike most northern temperate birds, survival of

juvenile and adult sociable weavers was similar. Survival was not affected by variation in food levels and did not differ significantly between years, although there was a negative effect of winter temperature. This suggests that the high survival in this species might result from a benign climate and easy access to food in winter. Juvenile survival is probably further enhanced by extended parental care and delayed dispersal.

Survival analyses also showed that, in both adult and juvenile sociable weavers, survival increases with body mass to some extent, but then declines, providing evidence for strong stabilising selection on body mass in this species. This pattern is unusual and might results from a trade-off between the risk of starvation at low mass and impaired performance at escaping predators at high mass.

Theory predicts that species with high survival and longevity inhabiting variable environments achieve maximum lifetime reproductive success through maximising the number of breeding events in life rather than through strong investment in current reproduction. To test this and further understand what limits reproductive effort in sociable weavers, I conducted brood size manipulations over two breeding seasons. I predicted that sociable weavers should refrain from increasing reproductive effort to raise an artificially enlarged brood. As predicted, sociable weavers did not work harder to raise enlarged broods and never fledged a fully enlarged brood, while fledging mass did not differ between enlarged broods and controls.

Sociable weavers seldom engaged in breeding activity in the first two years of life, yet they did not experience any obvious constraints on independent reproduction. Breeding conditions and reproductive success varied greatly during my study. I hypothesised that some individuals skip breeding under sub-optimal conditions to delay the cost of reproduction. I conducted an experiment where I reduced the cost of reproduction at some colonies by providing a food supplement at a negligible cost to the birds. The results obtained supported this hypothesis. The experiment caused a significant increase in breeding activity and a decrease in the number of helpers at the nests in food-supplemented colonies. Furthermore, yearlings occasionally bred in food supplemented colonies, but this was never the case in controls.

The results presented here suggest that the life history of the sociable weaver is primarily influenced by a benign climate leading to reduced mortality. This in turn should favour reduced fecundity and delayed maturity, with the latter creating the conditions for cooperative breeding to occur. At a proximate level, food availability plays an important role in determining clutch size and the decision of whether or not to engage in independent breeding.

Contents

Acknowledgements

First and foremost, I would like to thank my supervisor Morné du Plessis for his continuous support during these four years. I greatly appreciate the freedom Morné gave me to develop my own ideas, while always being there when I needed him.

This study would have not been possible without the collaboration of De Beers Mining Corporation who kindly provided access to Benfontein Game Farm.

The study would have not been the same if Mark Anderson hadn't initiated a capture-recapture study of sociable weavers at Benfontein in 1993. I'm very grateful for the opportunity of having been able to use this database and to build onto it. I'm also very grateful to Mark for always being extremely helpful regarding the sociable weaver study, for sharing his experience and for his efforts to provide us with a base at the Northern Cape Nature Conservation offices.

During this thesis I was funded by a doctoral scholarship from the program Praxis XXI, Fundação para a Ciência e Tecnologia (Portugal), which also paid laboratory costs. Additional funding came from the National Research Foundation of South Africa through a grant to Morné du Plessis.

My ideas on life history evolution and cooperative breeding were influenced by many people. Morné was an obvious influence and I thank him for many long and stimulating discussions. Also at the Fitz, Penn Lloyd shared most of my interests and I greatly benefited from our numerous discussions, from Penn's critical spirit and from his experience on arid region birds. During the 'cooperative breeding safari' organised by Morné in 1998 I had the opportunity of interacting with a distinguished group of scientists. In particular, I would like to thank Jan Ekman for important discussions on extended parental care and juvenile survival. During the 'safari' I also had the chance to meet Tom Martin and during this four years our sporadic interactions were extremely stimulating and mind-opening. I thank Tom for many discussions, for his critical and constructive spirit and permanent enthusiasm.

The analyses of the sociable weaver database (presented in Chapters 2 and 3), were the result of a collaboration with Charles Brown and Mary Bomberger Brown. I'm particularly grateful to Charles for introducing me to the capture-recapture techniques and for many constructive comments on these chapters.

Denis Lepage was of great help during the statistical analyses, always readily and painstakingly replying to my e-mails.

Claire Spottiswoode kindly read the thesis and spotted many English errors.

I had a great time working on this thesis, which was largely due to the wonders of life at Benfontein. A great number of people made Benfontein such a wonderful place.

First, I would like to thank my numerous volunteer helpers, without whom this work would have been literally impossible. In chronological order they were: Gisele Murrison, James Nicholls, Iain Barr, Machteld Verzijden, Jan Scholliers, Trish Pontynen, Dave Logan, Elsie Tack, Bart Verbraak, Maria Jovovides, Susie Molony, Anne Charmentier, Marc Pierard, Loïc Lesobre, Gabi Curti and Vanina Fiorini. Thanks for the hard work and all the fun we had.

Besides this army of workers, I had some recurrent helpers who provided very precious assistance, particularly with the ringing. Ronele Visagie was always willing to come and help and after four years was still showing the same enthusiasm! Mark Anderson always came out in the early mornings when we needed him. Andy Pierce was also extremely helpful and enthusiastic with the ringing and even spent many afternoons trying to improve our skills of taking birds out the nets. Martim Melo helped in various aspects of the fieldwork (including building the only snake protection fence that ever worked) and making many ringing mornings possible.

Then there was the more 'resident staff' at Benfontein: thanks Claire, Colleen and Trish for all the fun, for our long discussions, our sharing of exciting field observations, the sunsets at the koppies and... the cooking, of course!

Many visitors passed by Benfontein, which made it all even better: Martim, of course, Rémy and the regular supply of cheese (!!), Paula with a single but good supply of many things, Pierre-Yves and his enthusiasm, Albertine and our wonderful little trip with Claire, my parents and my brother who came to see a little bit of what I was up to, Dirk, Kirsten, Richard, Åsa, Denis and Nathalie...

I'm very thankful to the farm manager at Benfontein, Peter Gibbs, and his family, for always being extremely helpful with various issues. And Peter managed to never lose his calm while these hordes of volunteers and visitors were coming through the farm...

In Cape Town, I would like to thank all the staff and students who make the Fitz such a pleasant place to work at. In particular, Chris Tobler, Lionel Mansfield and Hillary Buchanan were always very helpful at solving all sorts of problems. Danelle du Toit always impressed me with her efficiency in running our excellent library, and her kindness.

I also made an incursion in the molecular biology lab. Even though the results of it are not presented in this thesis, I would still like to thank Martim, Jessica, Geeta and Colleen O'Ryan for guidance and advice in the lab, Claire for enduring part of it with me (and a great deal without me), and, of course, Elsie for her many hours extracting DNA and sexing all those weaver samples.

At UCT or outside, Carlos and Wendy, Colleen and Onno, Ross and Andrea, Christian, Åsa, Kirsten, Dirk, Richard and many others contributed to make life much more fun.

My dear distant friends always managed to be present during these years: Mixa e Zé, João, Alexandre, Júlia, Anabela, Claire, Rémy, Paula, Albertine...

Claire Doutrelant came all the way down to this side of the planet for a post-doc and worked with me on sociable weavers. This study benefited greatly from Claire's participation. We shared efforts in the field (where she gave an invaluable contribution), in the lab and during preliminary analyses, and I learnt the value of collaborating. Claire also read the thesis at different stages and made important comments. *Merci d'être venue mon amie! Merci d'avoir été là pour partager le ciel et les ourages de Benfontein, la mer du Cap, les hammam, et les nuits tranquilles à coté de la cheminé. Et merci surtout d'avoir toujours fais confiance a notre amitié.*

Why one becomes interested in science is probably not really known, but it might be reasonable to assume that, at least in some cases, one's parents play a part... In my case, I'm very thankful to my parents for the way I was introduced to the world around me. For the opportunity to grow up in close contact with nature, for our holidays exploring remote areas, and for always explaining things to me whether they related to vulcanoes, microbes or mechanics.

During these four years Martim has always been ready to discuss (and question) ideas, to help in the field and to read manuscripts. Martim also took on the painful task of formatting this thesis, which made it look very good and saved me lots of time. *Mais que isso, esteve sempre comigo, aturou as crises de stress, animou, ralhou, cozinhou... E o melhor de tudo foi o que nos divertimos.*

1

Introduction

Geographical variation is a striking aspect of life history traits of organisms. For example, in birds and mammals, fecundity increases with latitude, whereas this trend is reversed in some echinoderms and molluscs (Stearns 1992). Why should such variation occur? In the last two decades the burgeoning field of life history evolution has tried to understand what causes differences in life history traits at different levels. Theoretical and experimental work has shown the importance of extrinsic mortality sources in driving life-history evolution (e.g. Murphy 1968, Reznick *et al.* 1990, Charlesworth 1994). For example, when mortality patterns of guppies *Poecilia reticulata* were experimentally changed from high adult mortality to high juvenile mortality, this caused significant life history evolution in the population, with a concomitant decrease in reproductive effort of adult breeders (Reznick *et al.* 1990). In birds, however, life history evolution is generally attributed to variation in food availability (Lack 1968, Martin 1987, Stearns 1992). Specifically, where food availability is low, birds are expected to lay small clutches, which in turn should decrease the cost of reproduction leading to high adult survival.

Birds in the tropics and southern hemisphere regions, when compared to their northern temperate counterparts, are characterised by smaller clutches, longer developmental periods, extended parental care of juveniles, and higher adult survival

(Moreau 1944; Lack 1948; Skutch 1949; Rowley & Russell 1991; Martin 1996; Russell 2000; Ghalambor & Martin 2001). The latitudinal variation in avian life histories offers an interesting backdrop for studying life history evolution that has received surprisingly little attention (Rowley & Russell 1991; Martin 1996). Still, several hypotheses have been put forward to explain this pattern (see review in Martin 1996). In line with the predominant ideas on avian life history evolution, it has been suggested that reduced food availability in southern regions could lead to reduced fecundity, which would translate into higher survival through the trade-off between reproduction and survival (Lack 1947, 1968). Low food levels could also yield slower developmental periods (Ricklefs 1976, Martin 1987). Alternatively, food limitation could be achieved through reduced seasonality leading to reduced mortality in the south, which would maintain populations near carrying capacity increasing competition for resources (Moreau 1944; Ashmole 1963). In a highly competitive environment it should also be important to produce good quality young. Hence, long developmental periods could be a strategy to improve the immune system and resistance to diseases and parasites (Ricklefs 1992). Finally, if nest predation is higher in the tropics and southern temperate regions, this could favour small clutches through selection for reduced parental activity around the nest and saving energy for a high number of re-nesting attempts (Skutch 1949). High nest predation in the south, however, does not seem to favour extended developmental periods.

Recently, studies based on comparisons of North and South America, suggested that latitudinal differences in extrinsic mortality could explain the trend in life histories (Martin *et al.* 2000; Martin 2002). Adult survival is thought to be higher at low latitudes, due to a more benign climate that reduces winter mortality (Rowley & Russell 1991; Ghalambor & Martin 2001). According to life history theory, enhanced survival prospects of adults should favour reduced fecundity (Murphy 1968, Charlesworth 1994). High survival prospects also mean that parents should be less willing to risk their survival in favour of that of their young (Charlesworth 1994, Ghalambor & Martin 2001, Martin 2002). This could explain longer developmental periods in the south if parents invest little in young during the stages where their

probabilities of survival are low (Martin 2002). Still, parents could increase their investment in young that have good survival prospects (i.e. fledglings and immatures) through extended parental care and allowing young to remain in the natal territory. This could increase juvenile survival, and thus increase reproductive success, at low cost to parents (Martin 1996, Russell 2000; Ekman *et al.* 2001). In agreement with this hypothesis, it has recently been shown that tropical and south temperate birds provide extended parental care (Russell 2000).

To date no consensus has emerged on what are the main causes of latitudinal differences in avian life histories. This is partly due to a scarceness of studies conducted at low latitudes. As a result, many features of the breeding biology of southern species are not well known and comparisons of life history traits are inconclusive (Martin 1996).

The geographical differences in life histories also extend into the domain of sociality, with the highest frequencies of cooperative breeding birds being found in the tropics and southern hemisphere regions (Gaston 1978; Brown 1987; Arnold & Owens 1998). The geographical overlap suggests that a possible relationship might exist between life histories and sociality (the life-history hypothesis, Russell 1989). This hypothesis was recently tested by Arnold and Owens (1998), who showed a negative correlation between adult mortality and clutch size, and the incidence of co-operative breeding. Furthermore, these authors showed that cooperatively breeding species are not randomly distributed among families, with the proportion of cooperative breeders per family being correlated with a low family-typical value of annual mortality. The authors interpreted this as showing that low mortality predisposes a lineage to cooperative breeding, rather than the other way round.

The study of cooperative breeding has traditionally focused on the role of ecology (e.g., Ford *et al.* 1988; Emlen 1991; du Plessis *et al.* 1995). The most widely accepted framework to explain the occurrence of cooperative breeding is the 'ecological constraints' model formalised by Emlen (1982). According to this model, some aspects of the species ecology will lead to habitat saturation, limiting the opportunities for independent breeding. This will prompt young to delay dispersal,

which is the first step for cooperative breeding to occur (Emlen 1991; Hatchwell & Komdeur 2000). For example, younger birds in an obligate cavity-nesting species could be prevented from breeding independently by a lack of cavities, remaining at home until a suitable cavity becomes available (e.g. du Plessis 1992).

The life history hypothesis suggests a subtle twist in this traditional view of habitat saturation. According to this hypothesis, habitat saturation can be seen as consequence of differences in life history traits, and not some peculiar feature of the species ecology (Russell 1989; Arnold & Owens 1998). High survival should lead to low population turnover, creating competition (e.g. for breeding territories or mates), limiting the opportunities for independent breeding, and favouring conditions for cooperative breeding to occur. Therefore, this view implies that, at a proximate level, delayed dispersal should still be caused by habitat saturation.

A limited access to habitat has been shown to promote delayed dispersal (reviewed in Emlen 1991), but such an 'ecological constraint' fails as a general explanation (see review in Ekman *et al.* 2001). In particular, it fails to explain why some species do not delay dispersal although their habitat is saturated, why some species still delay dispersal even though apparently suitable habitat is available or, more specifically, why some non-territorial species where dispersal is not a requirement for breeding (e.g. colonial species) postpone reproduction and may engage in cooperative breeding.

In this thesis I investigate some factors that might act as selective pressures on the evolution of life history traits, delayed reproduction and cooperative breeding in the sociable weaver *Philetairus socius* (Family Passeridae, sub-family Ploceinae), a passerine endemic to the semi-arid savannahs of south-western Africa. This species seemed an ideal model in which to study life history and cooperative breeding for three main reasons. First, sociable weavers are non-territorial colonial nesters. This stands in contrast to most well studied cooperative breeders, which are group-territorial. This departure from the traditional cooperative breeding model could potentially allow insights into overlooked factors. Second, sociable weavers inhabit a highly fluctuating environment where rainfall, which is erratic and unpredictable, is

the main determinant of food availability (Maclean 1973; Lloyd 1999; Dean & Milton 2001). This allows the study of reproductive strategies in contrasting conditions as well as to understand the effect of food availability on reproductive traits. Third, sociable weavers are a common species within their distribution range, they are sedentary, and their nesting structures are easy to reach.

Here, I focus on investigating the relationship between life history traits and environmental factors, and on conducting experiments to test what seemed pertinent questions. The main objectives of this thesis were:

- To provide a sound description of the reproductive life histories of sociable weavers and their relationship to several environmental and social factors as a first step to understand the effects of the environment on the species life history.
- To produce robust estimates of juvenile and adult survival, and investigate their relationship to environmental factors in order to understand the role of possible extrinsic determinants of mortality.
- To investigate whether sociable weavers adopt a life history strategy different from that of northern temperate passerines in general, and what influences their allocating decisions.
- To investigate what factors might favour delayed reproduction in the sociable weaver and determine the relationship between delayed reproduction and cooperative breeding in this species.

OUTLINE OF THE THESIS

In chapter 2, I present a detailed account of the species reproductive life histories and factors that influence reproductive effort and reproductive success at a proximate level. Chapters 3 and 4 describe juvenile and adult survival. These chapters are the result of a collaboration with Charles R. Brown and Mary Bomberger Brown (University of Tulsa) set up to analyse an 8-year capture-recapture data base that was initiated by Mark D. Anderson (Northern Cape Nature Conservation Service) in 1993. In Chapter 3, the data set is used to investigate variation in annual survival of

juvenile and adult sociable weavers and the effects of rainfall and winter temperature, as potentially important extrinsic factors. Chapter 4 deals with the effect of body mass on juvenile and adult survival. Chapter 5 presents the results of a brood size manipulation aimed at investigating life history strategy and allocation decisions in sociable weavers. Chapter 6 deals with a food supplementation experiment that investigated the relationship between postponed breeding and the cost of reproduction in this species. Finally, in Chapter 7, all the results presented in this thesis are brought together and their implications for our understanding of avian life history evolution and cooperative breeding are highlighted.

The work presented in the different chapters is related, but each chapter was written as an independent paper that stands on its own. This approach is encouraged in the Science Faculty of the University of Cape Town, but regrettably results in a certain amount of repetition.

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2

The effect of nest predation, food availability and helpers on life history traits in the sociable weaver

In birds there are remarkable differences in life history traits between the Southern and Northern Hemispheres. Several hypotheses have been proposed to explain this pattern, but no general explanation has emerged. This is partly due to a paucity of detailed studies in the Southern Hemisphere. I conducted such a detailed study in order to determine which factors may explain variation in reproductive life history traits, juvenile dispersal and age of first reproduction in the sociable weaver *Philetairus socius*. Sociable weavers are colonial cooperative breeders endemic to the semi-arid savannahs of south-western Africa. Here I report the results of findings based on 100-150 nests per year from 18 different colonies during 3 consecutive years. Sociable weavers had extended breeding seasons (up to 9 months), laid relatively low but highly variable clutch size (3.3 eggs), a high number of reproductive attempts (up to 9 in the longest season), generally low dispersal, and reproduction in the first two years of life was rare. The proportion of nests with helpers varied from 30% to 82% of the nests between and within years. Nest predation was the main determinant of nesting failure, with an average loss of 70% of clutches. Snakes were responsible for the majority of nest losses. Rainfall was the main determinant of duration of the breeding season, variation in clutch size, and fledging success. Since rainfall was highly variable, reproductive success also varied greatly between (and within) years. The presence of helpers did not significantly increase reproductive success as measured here. Helpers tended to increase fledging mass when conditions were poor, but had no effect on brood reduction (which was common), and neither did their presence decrease the number of days between broods.

INTRODUCTION

In birds there is a well-known but poorly understood latitudinal trend in life histories. Birds in the tropics and Southern Hemisphere are typified by small clutches, long developmental periods, extended parental care and high survival (Moreau 1944; Lack 1948; Martin 1996; Russell 2000; Ghalambor & Martin 2001). Despite birds being relatively well studied, we still lack a general explanation for this pattern. This is partly because detailed accounts of factors that cause variation in reproductive parameters of Southern Hemisphere birds are scarce.

The life histories characteristics of southern birds have been attributed mainly to three hypotheses (see also Martin 1996). First, food levels could constrain fecundity if southern regions are less productive, or if low seasonality at low latitudes results in low winter mortality. This in turn would lead to higher population densities and increased competition for food during the breeding season (Moreau 1944; Ashmole 1963). Second, nest predation rates may be higher at low latitudes favouring smaller clutches, so that fewer chicks have to be fed, and thus reducing activity around the nest to avoid attracting predators (Skutch 1949). Finally, recent studies have suggested that latitudinal differences in life histories might be due to benign climates favouring extrinsic high survival in the South and leading to a reduction in reproductive effort (Martin *et al*, 2000; Martin 2002). This could be coupled with an increased investment in young to maximise juvenile survival, thus increasing reproductive success with no significant increase in reproductive effort (Martin *et al.* 2000; Russell 2000).

Thus far, no consensus has emerged on what could be the main factor(s) leading to the evolution of these differences in life histories. It is therefore important to conduct intensive studies over different seasons on poorly known southern species in order to understand the role played by the various factors.

I conducted a three-year study aimed at understanding the role played by different environmental and social factors on the reproductive life history of a cooperative passerine endemic to Southern Africa, the sociable weaver *Philetairus socius*. I depart from the traditional cooperative breeding model by studying a non-territorial, colonially-nesting cooperative breeder. In this species, shortage of

territories, nesting sites and other requisites for reproduction typical of cooperative breeders do not seem to play an important role.

Specifically, I investigate how reproductive effort and reproductive success are influenced by nest predation, food availability and the presence of helpers-at-the-nest, and I describe two important life history traits: juvenile dispersal and age of first reproduction. I discuss the findings in light of the main hypotheses put forward to explain the differences in life histories at low latitudes, and their implications for the evolution of cooperative breeding.

METHODS

Study area and species

The sociable weaver is a passerine endemic to southern Africa, with its distribution centred in the Northern Cape and Namibia in strong association with the arid savannahs typical of the southern Kalahari region (Maclean 1973a; Mendelsohn & Anderson 1997). Sociable weavers build a very large communal nest with separate chambers in which a pair (with their offspring or other birds) roost and breed (see page III). The nest is made mainly of *Stipagrostis* grasses and is built on a variety of sturdy structures, from *Acacia* trees to telephone poles (Maclean 1973b; Mendelsohn & Anderson 1997), but on our study area, the nests are almost exclusively constructed on *Acacia erioloba* trees. The colony can remain active for several decades, being occupied by successive generations of weavers, which continuously add to the structure (Maclean 1973b).

Sociable weavers weigh approximately 26-32g, and the sexes are indistinguishable in the field. They feed on a wide variety of insects (that make approximately 80% of their diet), but also on seed and other plant products (Maclean 1973e). Sociable weavers are colonial, cooperative breeders, and show great variation in colony size (2-500 individuals per colony; Maclean 1973b) and in the number of helpers attending a brood (0 to 9 helpers per brood; Maclean 1973c). The helpers are most commonly offspring of the breeding pair's previous broods, but unrelated birds

may also help (Maclean 1973c; Marsden 1999, C. Doutrelant & R. Covas, in prep.). Both males and females help (C. Doutrelant & R. Covas, in prep.). In a study in the south-western Kalahari Maclean (1973c) found that sociable weavers' breeding parameters were highly influenced by rainfall, which was the main determinant of food availability through its effect on insect and seed abundance. Hence, both breeding periods and clutch size were highly variable, with breeding activity lasting up to 9 consecutive months and clutches varying between 2-6 eggs.

The main nest predators are snakes, the boomslang *Dispholidus typus* and the Cape cobra *Naja nivea*, which regularly raid the colonies during the breeding season causing great losses of eggs and chicks (Maclean 1973d; Marsden 1999, this study). The pygmy falcon *Polierax semitorquatus* is another nest predator, which may remove chicks from inside the nest chambers (pers. obs.), although with markedly lower impact.

The study was conducted at Benfontein Game Farm, an 11000 ha farm situated about 6 km south-east of Kimberley, in the Northern Cape Province, South Africa (approx. 28°53'S, 24°89'E). Benfontein presents elements of the three main biomes that converge in the Kimberley area: Karoo scrub, grassland and Kalahari sands. The study site is situated in the south-eastern parts of Benfontein, on an area of approximately 20 Km^2. The vegetation here is Kalahari sandveld consisting of open savannah dominated by *Stipagrostis* grasses and the camelthorn tree *Acacia erioloba*. An abrupt change in soil type produces an equally marked change in vegetation that becomes mixed Karoo scrub and grassland to the north of the study area.

The farm has antelope and wildebeest populations that are hunted annually in winter. During the course of this study the farm held 1000-2000 springbok *Antodorcus marsupialis*, 500-700 blesbok *Damaliscus dorcas philippi* and 200-400 black wildebeest *Connochaetes gnu* (farm management, pers. comm.). The black wildebeest were prevented from grazing in the study area by a protection fence. Additionally, a herd of 30-50 cattle grazed occasionally in the study area. Other large mammals present that are not exploited for commercial purposes include smaller antelopes such as grey duiker *Sylvicapra grimmia* and steenbok *Riphicerus campestri*, and predators such as

the black-backed jackal *Canis mesomelas* or the insectivorous aardvark *Oryctorepus afer* and aardwolf *Proteles cristatus*.

The area is semi-arid, experiencing low and unpredictable rainfall (average 431±127 mm per year, C.V.= 35.4; Weather Bureau, Pretoria). The area is situated on the eastern end of the sociable weaver distribution range. To the west, the rainfall decreases even further, with some areas in the south-western Kalahari experiencing less than 200 mm per year (Weather Bureau, Pretoria). Most of the precipitation in the study area falls during the summer months, from September to April (Fig. 2.1).

The summer rainfall in the 3 years preceding this study was within the normal range of variation for the area (333-497 mm), with the highest total recorded in the summer of 1996-97. There was however a low rainfall summer in 1994-95 (263 mm) that might have been responsible for the fact that most birds seemed to have skipped breeding in 1994 (see also chapter 3).

Field methods

I conducted this study from May 1998 to September 2001. During this period, 1598 individuals were marked (adults and nestlings) with a uniquely numbered aluminium ring at 18-19 colonies. A significant proportion of adults in the population was already ringed as a result of a capture-recapture study initiated in 1993 (Chapter 3). All adults and nestlings near fledging date were also given a unique colour-combination. To track juvenile dispersal or to mark immigrants, the resident birds at the studied colonies were captured with mistnets twice a year (at the beginning and end of the breeding season).

I monitored individual nesting attempts of 240 pair-years. I excluded from analyses presented here those colonies or nests that were part of experiments in 1999-2000 (Chapters 5-6). All individual nest-chambers in every colony were given a number and individually identified with a coloured plastic tag (3.5 x 2.5 cm). During the breeding season, all nest chambers in each colony were inspected every 4-7 days to detect initiation of new clutches. The nest mass was reached from the roof of a pick-p truck or using a step-ladder (or both). To inspect the contents of each nest chamber I

used a small round mirror with a torch lamp fitted to it (Fig. 2.2). Sociable weaver eggs usually hatch asynchronously at 1-day intervals. Nests were visited daily near the hatching date until all chicks had hatched. The nestling period is 21-24 days (Maclean 1973c) and if disturbed from the 18th day onwards the chicks will usually fledge prematurely (pers. obs.). To avoid this, I visited the nests for the last time when the oldest nestling was 17 days old. On these occasions I measured mass, tarsus and wing length and recorded the number of nestlings present. Since the nest contents could not be verified closer to the fledging date, I assumed that the number of chicks present at 17 days was the number of young fledged from that nest.

To identify the individuals feeding at a given nest I conducted 1-2 hour observations for 2-6 days from under a hide placed 2-5 m from the colony. Sociable weavers seemed oblivious of the observer once under the hide. To be confident that the right nest was being observed, the observer would place the hide in a position from which it was possible to visualise the entrance of the nest chamber. From the hide, the nest could also be identified by the number on the tag and/or position in the colony, or in relation to other nests. The birds attending a nest were identified through their colour rings when they perched before or after entering the nest. I recorded the number of feeding visits to the nest when the nestlings were 8-12 days, a period during which the feeding rate is not affected by age (unpublished data). Observations of post-fledging feeding were conducted opportunistically at the colonies, since sociable weavers forage mainly on tall grass away from the colony.

To assess loss of eggs and chicks to predation, I recorded all encounters with snakes during visits to the colonies. A nest in a given colony was considered depredated if it was found empty on a visit following a day when I found a snake foraging or feeding at that colony. If no snake was seen at the colony on a previous visit, but the contents of two or more adjacent nests suddenly disappeared, these were also considered to have been depredated.

A number of studies have shown that rainfall is the major determinant of food availability for birds in the semi-arid and arid regions of southern Africa, since it has a strong influence on insect hatching and seed germination patterns (e.g. Maclean

1973c,e; Lloyd 1998, 1999; Dean & Milton 2001). I used rainfall data from the Kimberley airport (situated approximately 15 km from the study area) in 1998. In 1999-2001, I used a rain gauge to collect rainfall data in the study area.

Even though the breeding seasons always stretched into the following year I refer, for simplicity, to each breeding season by the year in which it begun. Thus 1999 refers to the breeding season that started in September 1999 and continued until May 2000. The breeding activity in 1998 was not monitored from the initiation of the season, so that year was excluded from the relevant analyses on reproductive success.

Statistical methods

The analyses were aimed at understanding the causes of variation in reproductive life history traits and breeding success. More specifically, I recorded clutch size, hatching success, fledging success, fledging mass, feeding rate, total number of clutches laid in a season, total number of chicks fledged and interval between nesting attempts. I used fledging mass as a measure of nestling condition instead of the commonly used residuals of body mass against a linear measure of body mass since my data did not meet the assumptions underlying the use of the residuals method (see Green 2001).

I collected data from pairs or groups that made multiple breeding attempts in a season and were often present for more than one year in the study. Mixed models are necessary to analyse such data appropriately, since they incorporate random as well as fixed effects and do not require equal sample sizes (Bennington & Thayne 1994). However, due to extremely high nest predation, the sample sizes decreased markedly at each subsequent phase of the nesting period. With small sample sizes it was not possible to continue using mixed models since some parameters could not be estimated. Therefore, with sample sizes below n= 100 I used a random number generator to select one nesting attempt per pair (or group) to include in the analyses. This decreased the sample sizes even further.

Normally distributed variables (e.g. fledgling mass) were analysed using general linear modelling, while proportion data (hatching and fledgling success) were analysed assuming a binomial distribution. The analyses of clutch size, which included a

random effect, were undertaken using the general linear modelling of SPSS 9.0, followed by post-hoc tests. All other variables were analysed using GLIM 3.77.

Modelling in GLIM or SPSS was begun with all factors and pertinent interactions. A final model was selected after sequentially dropping all non-significant terms. In GLIM, the significance of terms was determined by the change in deviance after the term was dropped from the model.

The following factors were considered in all models: rainfall, group type (pair or pair with helpers), brood number, and colony size. In preliminary analyses I also included 'year', but this factor was dropped from all analyses where it was not significant. Rainfall was used as a surrogate for food availability. Dean & Milton (2001) showed that rainfall in a given month was the main determinant of bird numbers in their area in the following month. Here, I used the total rainfall over the 30 days prior to the day when laying (clutch size) or hatching (hatching success) were initiated, or measuring the chicks took place (fledging success and fledging mass). The choice of a 30-day period was based on the work by Dean and Milton (2001) and field experience, since in the absence of follow-up rains, the vegetation starts drying out and insect abundance decreases approximately one month after the rains. I also conducted preliminary analyses using rainfall over other periods, but found the measure of rainfall used here to be the most informative. I considered three categories of rainfall: $<$50mm, 51-100mm, $>$100mm. To analyse the effect of helpers I used 'group type' (pair or group), since preliminary analyses showed that the variables studied did not have a directional linear response to number of helpers. Colony size was included as a categorical variable with 3 categories ($<$20, 20 – 40, $>$40). Since sociable weavers lay up to 9 successive clutches, a decline in clutch size or breeding success could take place as the season progressed. I included brood number as a multilevel (up to 8) categorical variable to investigate this possibility. To investigate the influence of nest predation on total number of breeding attempts, I analysed the nest predation events suffered by a given pair against their number of breeding attempts. More details about each analysis are given below.

RESULTS

In the three years of the study, sociable weavers started breeding in spring (i.e. from late August or September), with the duration of the breeding season being closely linked to duration and pattern of rainfall (Fig. 2.3). The percentage of individuals breeding in a given month was also influenced by rainfall in the previous month (Fig. 2.3). A substantial number of birds in all colonies never bred. In 1999 the percentage of birds breeding per colony varied between 43-83%; in 2000 it varied between 29-75%.

The proportion of nests attended by pairs with and without helpers varied between years. In 2000, 82% of the breeding pairs were assisted by helpers (n= 51). In 1999, there was also variation within the season. Initially, only 30% of the breeding pairs had helpers, but as the season progressed, some pairs successfully raised young that became helpers at subsequent broods, increasing the percentage of pairs with helpers to 46% at the end of the breeding season (n= 43).

Incubation usually (but not always) commenced with the laying of the first egg. The mean incubation period (defined as the period from the day the first egg was laid until the day before the first chick hatched) was 15.26 ± 0.99 (n= 56). The nestling period lasted 21-23 days, but fledglings returned to the nest and continued being fed there by the adults for up to a week. I observed adults feeding juveniles between 30-45 days after fledging on four occasions; juveniles continued to beg from adults for up to two months after leaving the nest.

Juvenile movements and age of first breeding

Young weavers always remained in their natal colonies for at least 4 months after fledging, and dispersal in the first year was rare. Of the 164 individuals ringed in the nest and re-captured one year later only 6% (11) had moved to another colony. Three of these birds were captured at their natal colonies early in the breeding season, only moving to another colony later on, suggesting that winter had been spent at home. All 11 young birds that dispersed in their first year had hatched in the first three

months of the previous breeding season. I never recorded dispersal of individuals that hatched after December.

Only 0.6% of birds ringed as nestlings were recorded to have bred in the following year (i.e. 1 out of 164 yearlings captured), and only 5% were recorded as breeders two years later (i.e. 4 out of 84 two-year old birds captured).

Total number of clutches and seasonal reproductive success

The number of clutches laid varied between years, with a maximum of nine clutches per female in 1999 versus a maximum of five in 2000 (Fig. 2.4). In both years, the number of successful broods raised was low (1999: 0.9 ±0.7; 2000: 0.6 ±0.6), and the maximum number of successful broods raised by any pair was three (Fig. 2.5). Within each year, the total number of broods laid was mainly determined by the number of nest predation events suffered by each pair, with individuals that had their broods depredated more often laying significantly more clutches (1999: $F = 46{,}31$, d.f.= 2, 32, $p < 0.001$; 2000: $F = 12{,}59$, d.f.= 1, 41, $p < 0.005$). In 2000 there was also a significant effect of colony size, with small colonies laying more clutches than big ones ($F = 6{,}289$, d.f.= 1,40, $p < 0.025$). The presence of helpers had no effect.

The total number of young fledged per pair also varied between years, but remained low even after an exceptionally good year such as 1999 (1999: 2.2 ± 2.0; 2000: 1.1 ± 01.2; Fig. 2.5). Within each year, the number of young fledged per pair was mainly determined by the nest predation events suffered by that pair (1999: $F = 29.18$, d.f.= 2,30, $p < 0.0005$; 2000: $F = 16.83$, d.f.= 1,40, $p < 0.0005$). In 1999 there was a non-significant trend for smaller colonies to produce more fledglings ($F = 3.25$, d.f.= 1,3, $p = 0.08$). Group type (presence or absence of helpers) had no significant effect in either year.

Predation rates

In 1999 I monitored a total of 481 nesting attempts, of which 381 (79%) failed. Of these, 360 failures (75%) could be attributed to predation with confidence. The other failures could also have been caused by nest predation, but this could not be

ascertained confidently. Nest abandonment could only be confirmed on one occasion. I thus considered nest predation rates for 1999 ranging between 75 and 79%. In 2000, I monitored 229 nesting attempts, of which 165 (72%) failed. Following the same reasoning as above, I considered predation rate to be between 60 and 72%. There was also variation in predation rates between colonies; in 1999 colony predation rates (defined as the fraction of the total of clutches initiated that were depredated) varied between 47 and 93%, and in 2000 between 48 and 100%.

Boomslangs *Dispholidus typus* and Cape cobras *Naja nivea* were the most important predators. Large snakes frequently depleted all nest contents in small and medium sized colonies. Snakes often remained at the same colony for several days or even weeks, moving regularly through the nest chambers to feed on new eggs or chicks. Thus even juvenile snakes caused severe loss.

Clutch size

Sociable weavers laid clutches of 2-4 eggs in 1998 and 2000 and 2-5 eggs in 1999 (mean 3.3 ± 0.7). Clutch size varied significantly with rainfall ($F = 9.48$, d.f.= 2, 206, $p < 0.001$; Fig. 2.7), increasing significantly with rainfall above 100 mm (Tukey test, $p < 0.001$). Factors such as brood number, group type, numbers of helpers and colony size, all had no effect on clutch size.

Hatching and fledging success

Hatching success did not vary with rainfall, group type, brood number, colony size or clutch size. There was a trend for groups to have higher hatching success than pairs after good rainfall, but this was non-significant (binomial model, interaction of rainfall with group type $\chi^2 = 5.67$, d.f.= 2, n= 67, $p = 0.06$). All eggs in a clutch hatched in 66% of broods (n= 132), and complete hatching failure was recorded in only one case.

Fledging success of non-depredated broods significantly increased from approximately 77% with rainfall below 100 mm to 100% when more rain fell (binomial model $\chi^2 = 5.62$, d.f. =1, n= 56, Fig. 2.7). Fledging success did not vary significantly with clutch sizes between 2 and 4, but decreased significantly in clutches

of 5 ($t = 1.86$, d.f. = 52, $p < 0.05$; Fig. 2.8), although sample size for the latter class was small ($n = 4$). All other factors and the interaction of rainfall with group type were non-significant.

Fledging mass

Fledging mass was generally positively affected by rain and negatively affected by the number of young fledging together. The general linear model showed a significant interaction between group type (i.e. pairs vs. groups) and the number of chicks fledged ($F = 4.89$, d.f. = 3, 39, $p < 0.01$; Fig 2.9a), but the effect of helpers was significant only with the presence of two ($t = 2.46$, d.f = 39, $p = 0.01$) and three ($t = 1.87$, d.f = 39, $p = 0.04$) nestlings. There was also a significant interaction between rainfall and the number of chicks fledging together ($F = 32.43$, d.f. = 6, 40, $p < 0.001$; Fig 2.9b), with a tendency for chicks to fledge lighter with lower rainfall ($t = 1.52$, d.f. = 40, $p = 0.06$). Finally, I found a non-significant trend for helpers to increase fledging mass when rainfall was lowest ($F = 3.16$, d.f. = 2, 36, $p = 0.06$; Fig 2.9c).

Feeding rate

I defined feeding rate (FR) as the number of feeding visits to the nest per hour when the nestlings were 8-12 days old (pin break normally takes place at day 8). I investigated how FR varied with the number of nestlings, group type, and rainfall of the previous month (as an indicator of food availability). The average overall feeding rate in this population was 13.4 ± 5.3 (pairs: 12.9 ± 6.0; pairs with helpers: 13.6 ± 5.1). In an initial analysis, including the whole data set ($n = 48$), the number of nestlings significantly influenced the number of feeding visits per hour ($F = 5.128$, df = 3,47, $p < 0.01$); the other variables being non-significant. To control for number of nestlings, I repeated the analysis with a subset of the data including only nests with two and three nestlings ($n = 29$). In this new analyses, the number of nestlings became non-significant ($F = 0.169$, d.f. = 1,29, $p = 0.684$). However, there was a significant effect of group type, with nestlings fed by groups receiving more feeding visits than those fed by pairs (groups: mean = 14.1 ± 3.9; Pairs: mean = 10.3 ± 3.6; $F = 5.985$, d.f =

1,29, P= 0.02). The feeding rate did not seem to be affected by food availability, since the rainfall factor was not significant.

Interval between nesting attempts

The number of days between the termination of a nesting attempt and the initiation of laying of the next clutch in the same season depended on the fate of the previous brood. The interval was shortest if the brood failed during incubation (10 ± 5.3 days, n= 14), intermediate when the brood failed during the nestling phase (14 ± 10.7 days, n= 15) and longest after a successful brood (33.5 ± 16.2 days, n= 25; χ^2= 240, d.f.= 2, p< 0.001, n= 44; Fig. 2.10). There was no effect of group type or rainfall on the interval between nesting attempts when controlling for the effect of predation by using only the interval after successful broods.

DISCUSSION

Sociable weavers share most features characteristic of 'southern' birds. They had long incubation and nestling periods, long breeding periods with multiple breeding attempts and long periods of dependency of young. Dispersal was low, as is characteristic of other colonial nesting species. More interestingly, reproduction in the first two years of life was virtually non-existent. The clutch size found here (3.3) was relatively small compared to most northern temperate passerines of similar size. It was, however, slightly larger than that of many other southern species. For example, Rowley and Russell (1991) found mean clutch sizes for both Africa and Australia to be 2.7 to 2.8.

Nest predation

Nest predation varied between years, with 60-79% of the nesting attempts in a season being depredated. This feature seems widespread among sociable weavers as high nest predation by snakes has also been reported in two other studies (Maclean 1973d; Marsden 1999).

Skutch (1949) suggested that small clutches at low latitudes could be due to higher nest predation rates in these areas. He assumed that nest predators cue on parental activity to find nests. Therefore, in areas with high predation rates, birds should lay smaller clutches in order to reduce activity around the nest. This mechanism cannot, however, apply to colonial species such as the sociable weaver, since the activity generated by multiple breeders (and their helpers) and the large colony structure make them very easy to detect. Another mechanistic hypothesis for how nest predation may affect clutch size suggests that under high nest predation parents should reduce clutch size to save energy for future nesting attempts. This has been demonstrated experimentally by Slagsvold (1984) and correlatively by Martin (1995). The results obtained here, showing that the interval between nesting attempts increased with stage of loss, provide some support for the possibility that this mechanism might be acting in the sociable weaver. More generally, nest predation is expected to influence life history evolution. Theory predicts that nest predation, through increased mortality of young, should select for delayed maturation, reduced reproductive effort, and increased adult survival, since low reproductive success should favour an increase of reproductive life-span to maximise the number of breeding episodes (Stearns 1992; Charlesworth 1994; see also Reznick *et al.* 1990).

It is not clear to what extent nest predation is higher in southern regions. Nest predation rates could be higher in the south if these areas are less impacted by humans and hold higher numbers of predators (see Martin & Clobert 1996). However, different studies at different latitudes have reported very diverse predation rates (reviewed in Martin 1996). The long incubation and nestling periods reported here (and in other southern species; see Martin 1996) are also contrary to the predicted effect of high nest predation rates as a major evolutionary factor across latitudes. Recently, the nest predation hypothesis was rejected as an explanation for smaller clutches in a comparative study of bird communities in Argentina and Arizona (Martin *et al.* 2000). Nest predation was lower in Argentina where clutch size was also lower. In contrast, predation rates seem generally high in southern Africa. Data available on 51 *Brachystegia* woodland species gives a median of 71% eggs lost to

predation (Vernon 1984). Another study from the arid south-western Africa also reported considerably high predation rates (e.g., larklike bunting *Emberiza imbetuani* 96%, rufouseared warbler *Malcorus pectoralis* 51%, chat flycatcher *Malaenornis infuscatus* 65%, Cape sparrow *Passer capensis* 80%; Lloyd 1998). Therefore the effects of nest predation on the evolution of life histories of southern African birds probably deserve further study.

Food availability

Variation in food availability is another factor commonly advanced for explaining variation in most life history traits (Lack 1968, Martin 1987). Variation in food availability was examined in this study through the variation in rainfall, since in the arid to semi-arid subtropics rainfall is the main determinant of plant germination and insect abundance (Maclean 1973c,e; Lloyd 1999; Dean & Milton 2001; see also Methods section).

Sociable weavers' breeding cycle in my study site was closely linked to rainfall. When nests escaped predation, variation in rainfall was the main predictor of variation in reproductive effort as reflected by clutch size, and reproductive success as reflected by fledging success and fledging mass.

Martin (1996) suggested that possible effects of food limitation on life histories could be best explained by traits such as number of nesting attempts per year and interval between nesting attempts. The number of nesting attempts and duration of the breeding season in this study was closely linked to duration of rainfall. Since nesting conditions are so variable and unpredictable for sociable weavers, one would expect such an opportunistic character of breeding activity in relation to the environment. Sociable weavers' breeding period lasted between five and nine months, with up to 9 nesting attempts in a long season, and a maximum of 3 successful broods. Such extended breeding periods certainly differ from the short seasons of northern temperate passerines, which also do not have the time for as many nesting attempts. The fact that sociable weavers seem to be able to remain in breeding condition for such extended periods seems to disagree with the hypothesis of lower food levels in

this region. However, the difference in the pattern of resource abundance between the two regions is so marked that a simple comparison of duration of breeding periods and number of nesting attempts might yield equivocal results.

The interval between nesting attempts in the sociable weaver (on average 10 or 14 days, depending on whether the brood was depredated during incubation or nestling stage) was longer than the typical interval of north temperate species (5 to 9 days), but similar to that of other southern temperate (5 to 14 days) and tropical species (14 days; reviewed in Magrath *et al.* 2000). The mean interval after a successful nesting event in sociable weavers (35 days) was also substantially longer than what has been reported for northern temperate species (i.e. around 8.5 days), but similar to southern species (21 to 29 days; reviewed in Magrath *et al.* 2000). The longer interval of southern species could reflect higher energetic constraints in the south. However, I found no effect of rainfall on the interval between nesting attempts. Magrath *et al.* (2000) suggested that southern birds might reassess conditions for breeding before they attempt another clutch. This hypothesis seems plausible in the south, where breeding periods are elongated and seasonal decline in resources does not seem as marked as in northern regions, therefore leaving more time to renest (e.g. Rowley and Russell 1991, Magrath *et al.* 2000). Furthermore, northern species are generally short-lived, which might favour their decision of attempting another brood even in sub-optimal conditions, since they might not live long-enough to breed again (see Charlesworth 1994). On the other hand, the longer renesting interval of southern birds after a successful attempt might also be due to the prolonged parental care given to young (e.g. Magrath *et al.* 2000). Alternatively, it has been recently suggested by Martin (2002) that longer-lived southern species should favour own survival in relation to increased investment in reproduction. According to this view, the longer intervals of southern species could therefore be seen as parents minimising risk to them selves from the cost of reproduction by spending more time recovering the energy spent during prior reproduction.

Food availability might explain why smaller colonies laid more clutches in 2000 (a relatively poor rainfall year). High numbers of conspecifics with similar feeding

requirements may deplete localised resources, forcing residents to go farther away to find food, or to spend longer searching for food in one area (Brown & Brown 1996). Alternatively, this result could be a consequence of poorer adult condition in larger colonies due to higher parasite loads (Marsden 1999), but that was not investigated in this study.

The capacity of birds to adjust reproductive effort and reproductive success to food availability has been widely demonstrated by studies of birds in the Northern Hemisphere (e.g. Bryant 1975; Jarvinen & Vaisanen 1984; Oro *et al.* 1999). The present study is one of the few to show the effect of food availability on reproductive life histories and reproductive success of a southern temperate passerine. Compared to northern birds, the extent to which sociable weavers vary most of their breeding parameters, such as clutch size and number of breeding attempts in one season, is rather unusual and might reflect an adaptation to a highly fluctuating environment.

It is usually accepted that, if food levels are low, fecundity is constrained, which is then expected to result in increased survival through a decrease in the cost of reproduction (Lack 1968; Martin 1987; Stearns 1992), and hence possibly explain the life history pattern in the south. However, the simple observation that fecundity and survival co-vary does not allow any conclusions regarding whether selection is acting on fecundity or survival. For example, if adult survival is high due to extrinsic factors, such as benign climate and high food levels in winter, life history theory predicts that fecundity should be reduced and maturity delayed. Furthermore, if fecundity is determined by food availability, the reproductive effort (the proportion of total energy reserves that is devoted to reproduction) should not decrease when fecundity decreases, in which case it would not be expected that survival should increase (Martin 1995).

An alternative hypothesis suggests that low fecundity and high survival can be favoured under high environmental variation. This 'bet-hedging' strategy reduces the risk of low success in a bad year, while increasing iteroparity and the chances of breeding in a good year (Philippi & Seger 1989; Stearns 1992: see also Boyce & Perrins 1987). This study showed that reproductive parameters of sociable weavers at a

proximate level are greatly influenced by rainfall, which is highly unpredictable, and hence that this mechanism could be acting in the study population. Further experimental work is required to distinguish between these different life history strategies.

Helper effect

In cooperative breeders, the presence of helpers-at-the-nest can have a marked effect on reproductive success and reproductive life histories (reviews in Emlen 1991, Cockburn 1998). In a variable environment with low reproductive success, helpers could potentially play an important role in alleviating the workloads of parents, thus promoting their survival, or in providing extra food when conditions are bad. Yet, I found that helpers had no clear positive effect on the parameters studied here. There was a significant increase of feeding rates to the nests, but this did not translate into any obvious increase in success. In fact, despite the positive effect of helpers on nestling mass, this was not significant when the number of chicks present was maximal, even though fledging mass decreased with the number of nestlings. Still, this effect might be important, since juvenile survival increases with mass to a certain extent (see chapter 4). Helpers did not increase fledging success even though brood reduction was common, neither did their contributions decrease the number of days between broods.

The search for the adaptive basis to cooperative breeding has resulted in a long list of possible benefits for both helpers and breeders (reviewed by Emlen 1991; Cockburn 1998). Since the helpers are often related to breeders, this has encouraged the idea that kin selection has played a major role in the evolution of cooperative breeding (Emlen 1991, 1997). The presence of helpers could increase the production of non-descendent kin by increasing the breeder's reproductive success. Still, some studies have found that the presence of helpers did not increase the breeders' reproductive success (reviewed in Cockburn 1998; Hatchwell & Komdeur 2000). This study provided weak support for the kin-selection hypothesis, but only further work could confirm it. In particular, it would be important to control for parental quality

in order to distinguish between parental and helper effect (e.g. Legge 2000) and to confirm that higher fledging mass increases survival and recruitment probabilities. The presence of helpers could also increase breeders' reproductive success if it contributes to alleviate their workloads and increase their survival. There is some suggestion, albeit weak, that sociable weaver males might decrease their feeding rates in the presence of helpers (Marsden 1999), therefore the enhanced survival possibility should be further investigated.

Dispersal of young and age of first reproduction

Young sociable weavers received extended parental care, and could be fed for over a month after fledging. Dispersal by juveniles in this population was low and almost never happened in the first year. High philopatry seems a common feature of colonial species, whether cooperative or not (e.g. Emlen 1991; Møller 1994; Brown & Brown 1996). Breeding activity in sociable weavers was rare in the first two years of life. This delayed onset of breeding by sociable weavers contrasts markedly with most northern temperate passerines, where reproduction usually commences in the first year (e.g. Newton 1989). Still, it seems common in cooperative breeders and possibly other southern temperate birds (e.g. Brown 1987; Russell 1989).

Extended parental care and occupation of natal territories by young is a common feature of tropical and southern temperate birds, in contrast to northern temperate regions, where young associate with the parents for less than a month in the majority of species (Russell 2000). Although delayed dispersal in cooperative breeders has usually been explained through some type of 'environmental constraint' that prevents young from breeding independently (Brown 1987; Emlen 1991), evidence has been accumulating that there can be clear benefits of remaining in the natal territory even if potential benefits of helping are excluded (Ekman *et al.* 2000; Green & Cockburn 2001). This possibility might apply to sociable weavers, since no obvious ecological constraints on independent reproduction can be identified in these species. Sociable weavers may become breeders at the natal colony, and shortage of mates does not seem to occur, since the sex ratio is approximately even (Doutrelant &

Covas in prep.). However, in a highly variable environment, where reproductive success is low, delaying maturation might be advantageous, since it may increase survival (Charlesrworth 1994), and hence potentially increase lifetime reproductive success by increasing the number of breeding events in life (Stearns 1992, Ekman *et al.* 1999).

Concluding remarks

This study showed that sociable weavers have a breeding cycle characteristic of 'southern' birds, which is markedly different from that of northern temperate birds. Perhaps the most noteworthy result of this study is the way in which reproductive output varied in such a marked and unpredictable manner between years due to variation in rainfall and nest predation. Unpredictability of reproductive output may select for an increased life span, favouring delayed maturation, and reduced fecundity (Schaffer 1974; Schultz 1991; Stearns 1992; Charlesworth 1994). While further descriptive and experimental work is needed to understand the importance of food availability (including seasonal pattern of resources), nest predation and extrinsic mortality in shaping life histories of southern birds, it might also be relevant to investigate the effects of environmental unpredictability.

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FIGURES

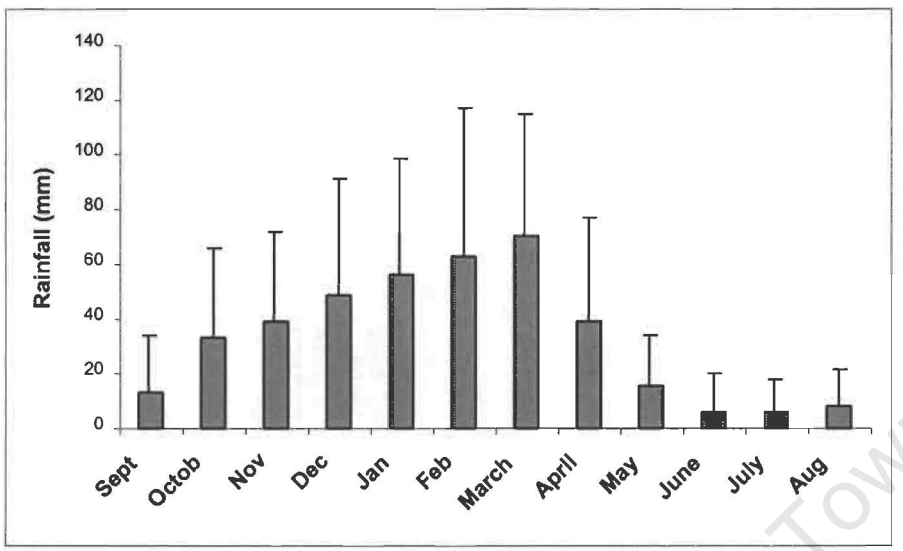

Fig. 2.1. Monthly rainfall at Benfontein Game Farm from 1900 to 1995. Bars represent mean and SE of data.

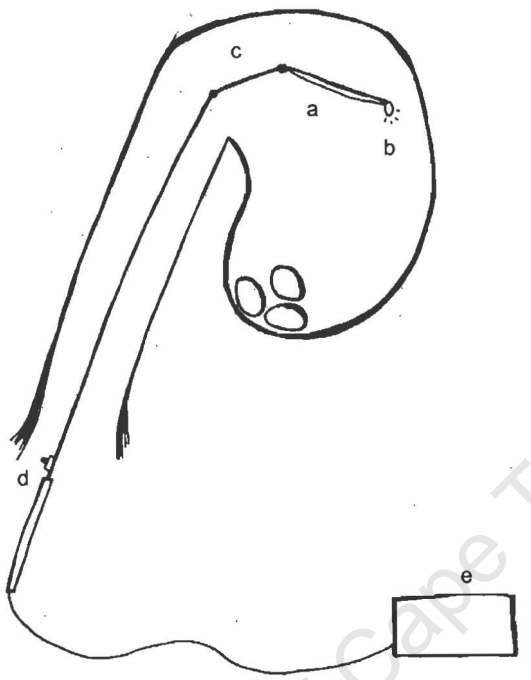

Fig. 2.2. Diagram representing a transversal section of a nest chamber with the mirror (a) and lamp (b) inserted. The mirror is placed at the end of an articulated handle (c). The lamp is operated through a switch (d) and the energy is provided by four batteries (e).

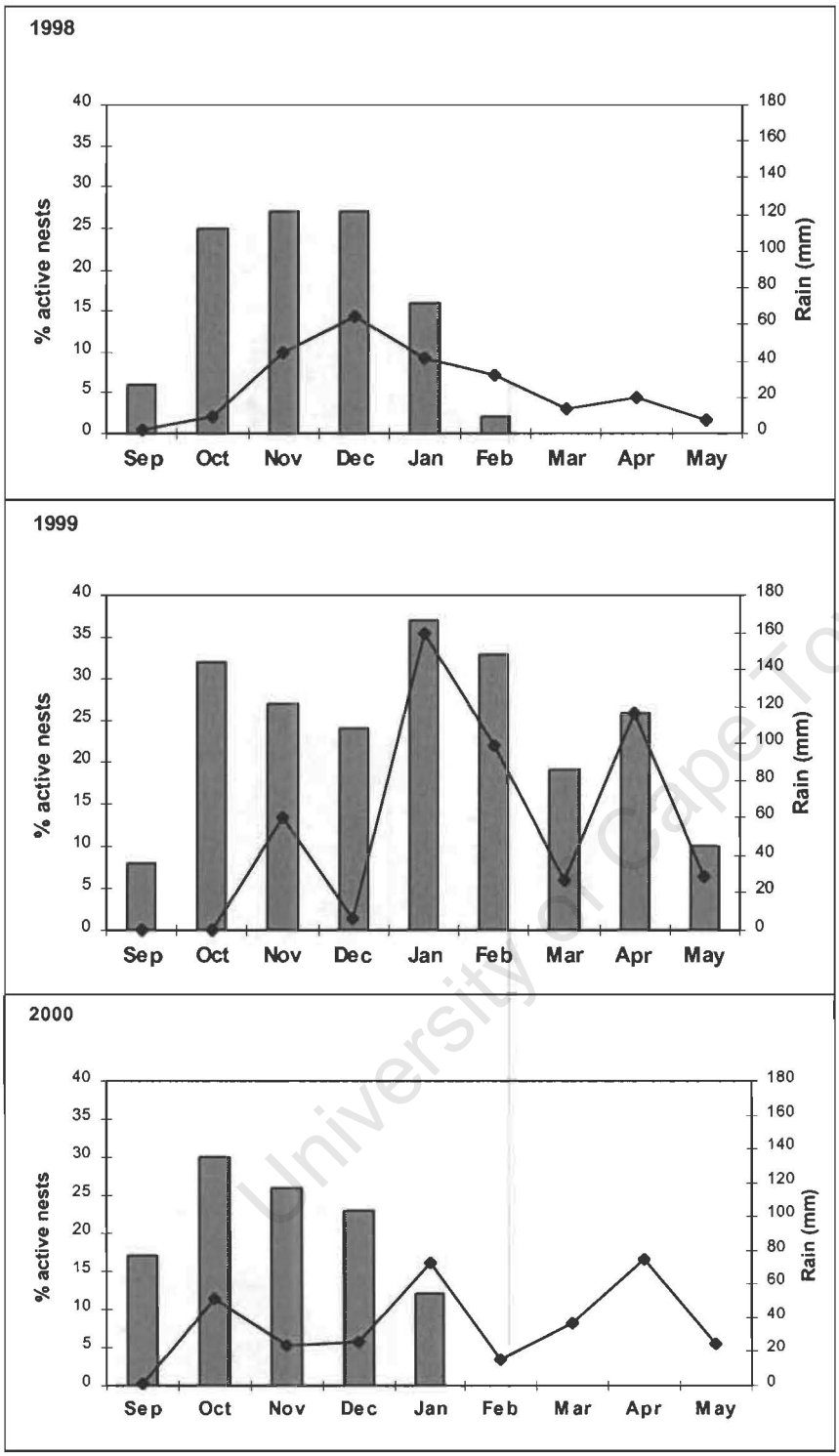

Fig. 2.3. Monthly nesting activity (% nests active; bars) and rainfall of the previous month (in mm; line) during the three breeding seasons 1998-2000. Nesting activity in Sep. and Oct. 1998 was estimated retrospectively using the number of young present in the population from November onwards; thus the values presented here might be an underestimation.

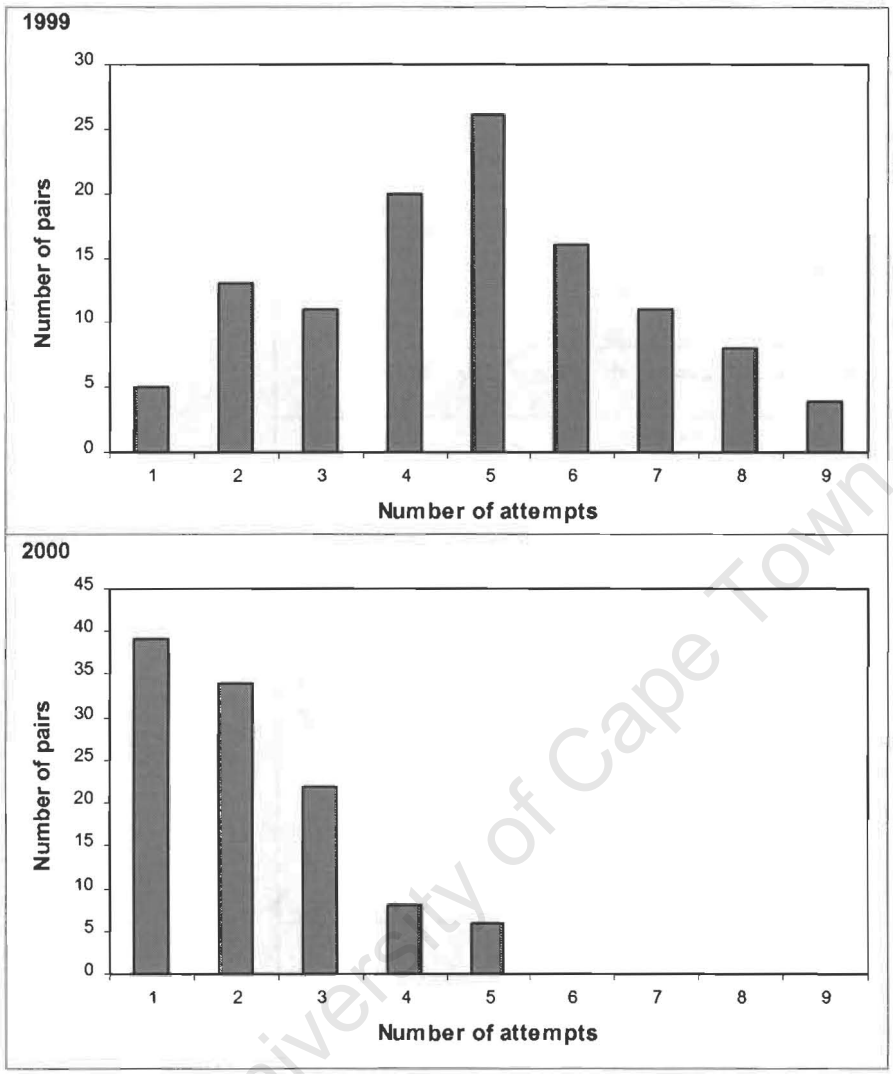

Fig. 2.4. Number of attempts made per breeding pair during the 1999 and 2000 breeding seasons.

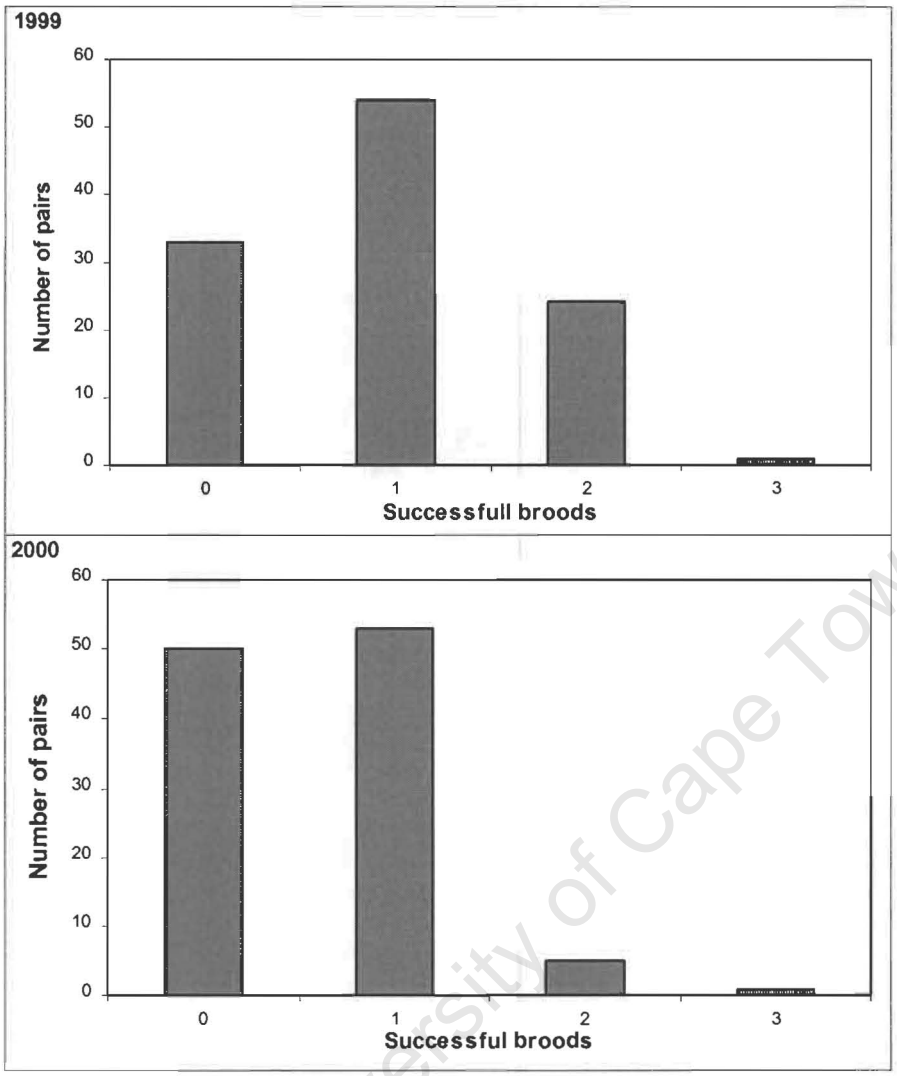

Fig. 2.5. Number of successful broods raised per breeding pair in 1999 and 2000. Bars represent the total number of pairs raising 0, 1, 2 or 3 successful broods in each year.

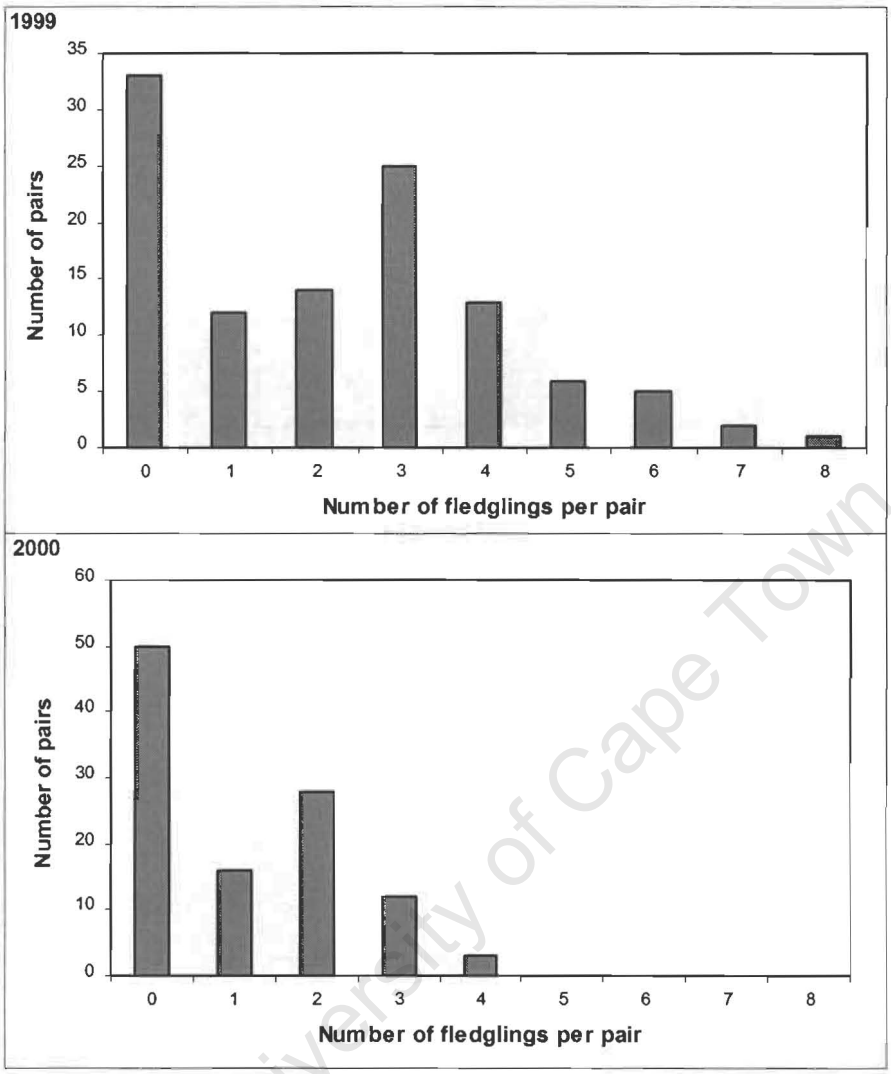

Fig. 2.6. Total number of young fledged per pair in 1999 and 2000 breeding seasons. Bars represent the total number of pairs raising the number of fledgling indicated on the x axis.

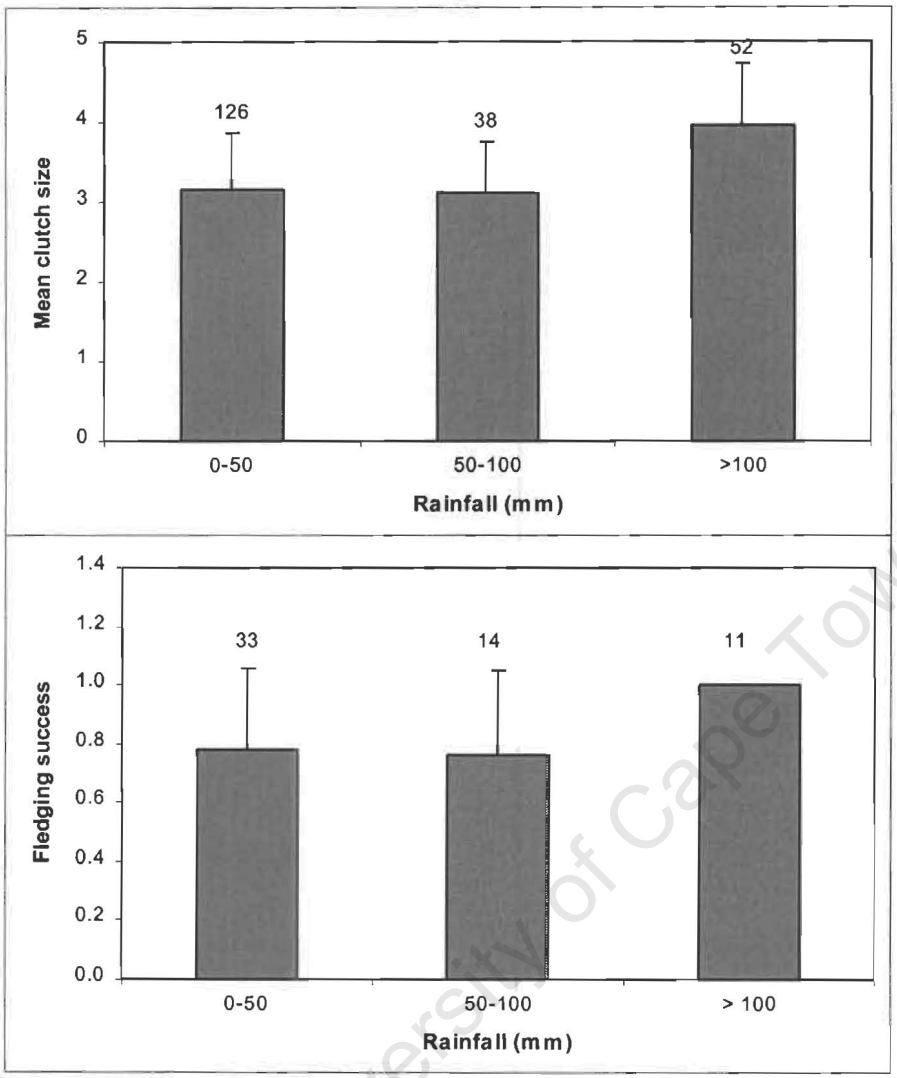

Fig. 2.7. Mean clutch size and fledging success in relation to rainfall. Bars represent mean and SE of data. Sample sizes are given above the bars.

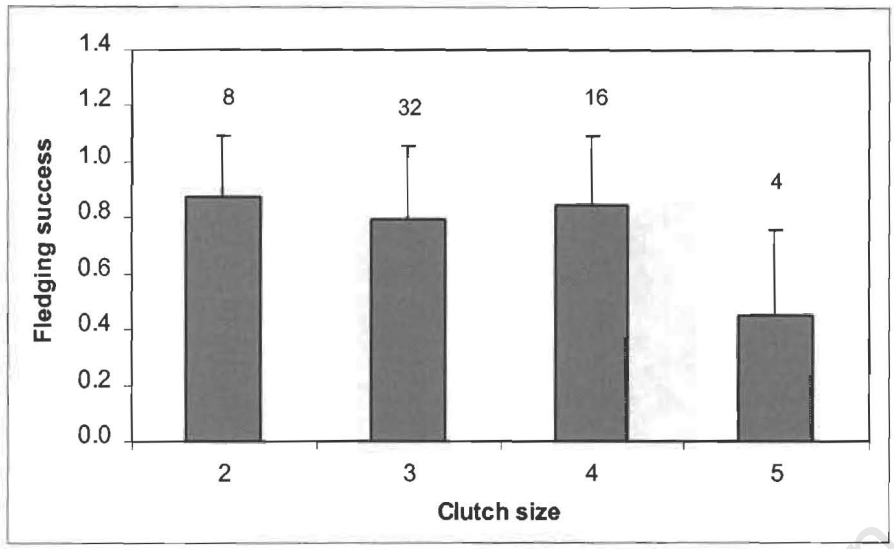

Fig. 2.8. Fledging success (fraction of hatchlings that fledged) in relation to different clutch sizes. Bars represent mean and SE of data. Sample sizes are shown above the bars.

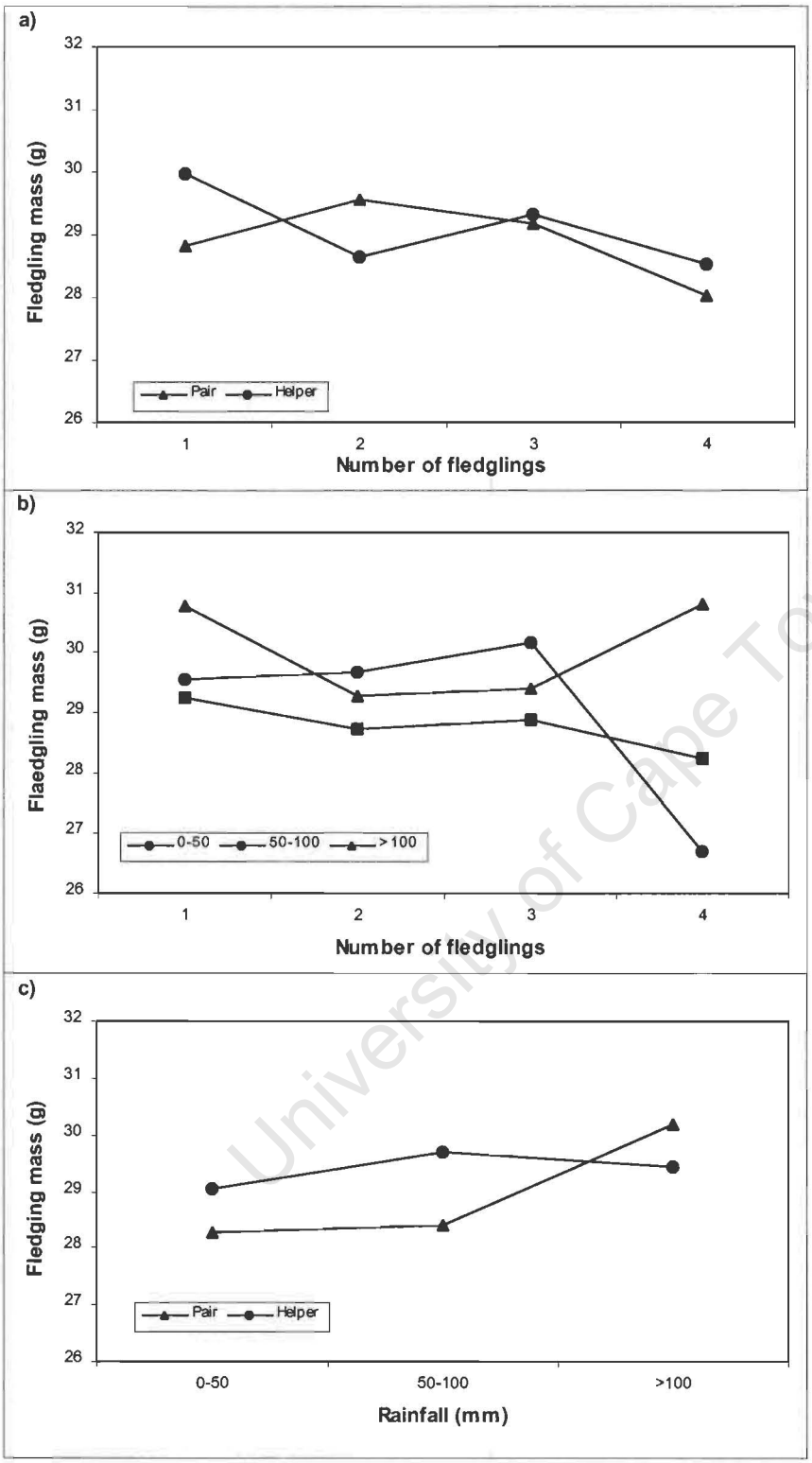

Fig. 2.9. Factors affecting fledging mass. a) interaction of rainfall with number of chicks fledging together; b) interaction of group type (pair or group) with number of chicks fledging together; c) interaction of group type (pair or group) with rainfall.

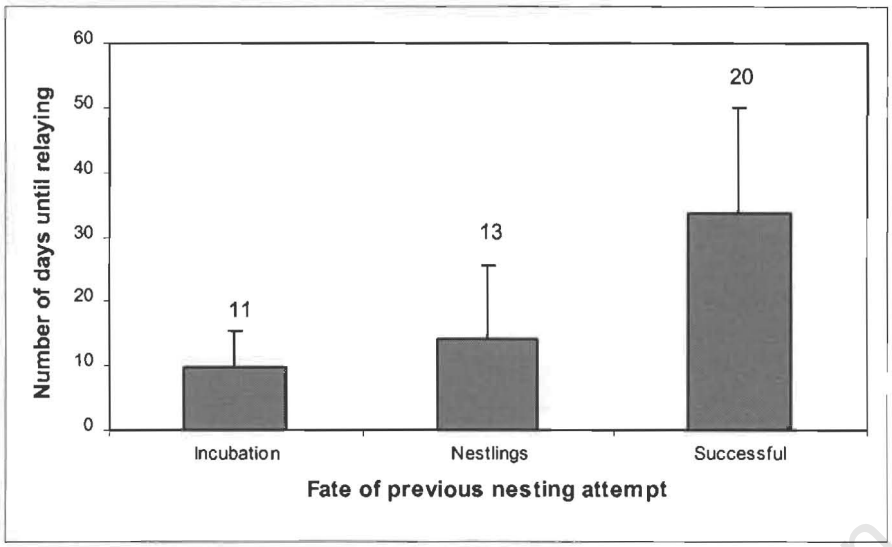

Fig. 2.10. Interval between breeding attempts according to the fate of the previous clutch. Incubation and nestling refer to when the nest failed; successful means the parents fledged at least one young. Bars represent mean and SE of data. Sample sizes are shown above the bars.

3

Juvenile and adult survival in a southern temperate colonial cooperative breeder, the sociable weaver

Latitudinal differences in survival rates of passerine birds are believed to result from environmental factors such as food availability or winter conditions, although little is known in general about annual survival rates of southern temperate birds. We use capture-recapture analyses to obtain juvenile and adult survival estimates over an 8-year period in a population of sociable weavers *Philetairus socius*, a colonial, cooperatively-breeding passerine of southern Africa. Annual survival probability was relatively high (0.66). In contrast to northern temperate passerines, juveniles and adults had similar survival probabilities and survival rates did not vary significantly between years. However, there was an effect of winter temperature, with survival generally increasing with average minimum winter temperature but declining in the warmest year. This result is probably related to thermoregulation. Survival was not affected by rainfall, an index of food availability. Relatively high survival rates in sociable weavers probably result from a benign climate and easy access to food in winter. Juvenile survival is also enhanced by prolonged parental care and delayed dispersal. These findings are consistent with recent models on the evolution of avian life histories at low latitudes.

INTRODUCTION

Age-specific mortality patterns and their response to environmental variation are central in understanding life history evolution (Stearns 1992; Charlesworth 1994). Yet, these life history traits are often poorly known due to methodological challenges associated with long-term marking and monitoring of individuals. In birds, this is particularly true of populations in the tropics and Southern Hemisphere, for which survival rates estimated with robust approaches are rare. Birds in the south are generally characterised by smaller clutches, longer developmental periods, and higher adult survival than their northern temperate counterparts (Rowley and Russell 1991; Martin 1996). These differences could be due in part to benign climates favouring higher adult survival in the south. According to life history theory, higher adult survival would favour reduced fecundity with increased investment in fewer young (Williams 1966; Charlesworth 1994; Martin 2002). Juvenile (i.e. post-fledging) survival should also be high at low latitudes due to the increased investment in young (Martin 1996; Martin *et al.* 2000; Russell 2000). It has recently been shown that species in the tropics and southern temperate regions do indeed provide extended parental care compared to northern temperate ones (Russell 2000). However, whether these differences in behaviour translate into higher survival in the south remains largely unknown, since juvenile survival has received little attention in most field studies.

The belief that tropical and southern populations experience higher adult survival than their north-temperate counterparts (e.g. Moreau 1944; Cody 1966; Ricklefs 1973) has recently received empirical support (Johnston *et al.* 1997; Ghalambor & Martin 2001; Peach *et al.* 2001), although it remains largely unknown how survival at low latitudes varies between years and how it is affected by environmental factors. Passerine survival can be affected by food availability (Jansson et al 1981; Newton 1998) and the severity of winter (McNamara & Houston 1990; Cuthill & Houston 1997). However, most tropical and southern temperate regions experience mild winters, which probably support relatively high food levels (Oatley 1982; Rowley & Russell 1991) and better weather conditions than in northern regions.

Studying how survival in the south is affected by food availability and weather variables would help in understanding the mechanisms regulating survival at low latitudes.

This paper investigates juvenile and adult survival in the sociable weaver *Philetairus socius* and how it is affected by food levels and winter conditions. Sociable weavers are colonial cooperative passerines endemic to the semi-arid savannahs of southern Africa. The latitudinal trend in avian life histories would predict higher adult survival in sociable weavers than in most north temperate passerines. High juvenile survival should also occur because, besides benefiting from the factors that might increase adult survival, young in this sedentary species receive extended parental care and remain in the natal colony for at least four months (Chapter 2). Sociable weavers are suitable for studying environmental factors and survival because they inhabit a highly fluctuating environment, where rainfall, which is variable and often low, is the main determinant of food availability and reproductive effort (Maclean 1973c; Lloyd 1999). Winters in our study area are usually sunny with mild daytime temperatures. However, night-time temperatures can drop to several degrees below zero, representing a severe cost in terms of thermoregulation (White *et al.* 1975; du Plessis & Williams 1994). This study aims to 1) examine the prediction that juvenile and adult survival in the sociable weaver should be high, 2) investigate temporal variation in survival, and in particular, 3) how survival is affected by two potential environmental constraints: winter temperature and rainfall.

METHODS

Study species

This study was conducted at Benfontein Game Farm, situated about 6 km south-east of Kimberley, in the Northern Cape Province, South Africa (approx. 28°53'S, 24°89'E). The vegetation in the study area consists of open savannah and is dominated by *Stipagrostis* grasses and the camelthorn tree *Acacia erioloba*. The area is semi-arid, experiencing low and unpredictable rainfall (average 431±127 mm per year; Weather

Bureau, Pretoria), with most of the precipitation falling during the summer months from September to April. The daily temperature ranges are typically high, with hot days and cool/warm nights from October to March (approx. 8-40° C) and mild days and very cold nights from May to September (approx. -8-25° C)

The sociable weaver is endemic to southern Africa, with its distribution centred in the Northern Cape and Namibia in strong association with southern Kalahari vegetation (Maclean 1973a; Mendelsohn & Anderson 1997). Sociable weavers weigh between 26-32 g, with the sexes being indistinguishable in the field. Sociable weavers feed predominantly on insects but also on seed and other plant products (Maclean 1973d). They are colonial, cooperative breeders and show great variation in colony size (2-500 individuals per colony; Maclean 1973b) and in the number of helpers attending a brood (up to 9 helpers per brood; Maclean 1973c). These weavers build a very large nest with separate chambers in which a pair (with their offspring or other birds) roost and breed. The nest is built on a variety of sturdy structures, from *Acacia* trees to telephone poles (Maclean 1973b; Mendelsohn & Anderson 1997). On Benfontein the nests are constructed on *Acacia erioloba* trees. The colony can remain active for several decades, being occupied by successive generations of weavers, which continuously add to the structure (Maclean 1973b).

Sociable weavers can breed aseasonally in response to approximately 20 mm of rain (Maclean 1973c). Rainfall is also a major determinant of the duration of the breeding period, number of broods (1- 8), and clutch size (2- 6; Maclean 1973c). In our study area, weavers usually start breeding in September or October, and the breeding season can last between three and nine months.

Field methods

From August 1993 to November 2000 a capture-mark- recapture study was conducted at Benfontein. The study area contained 24 sociable weaver colonies. At 15- 18 of these, the residents were captured twice a year. During the first five years, the capture effort was distributed throughout the year by capturing the birds in 1-2 colonies each month. Beginning in mid-1998, we concentrated the capture efforts during 1-2

consecutive months at the beginning and end of the breeding period. The birds were captured with mist nets placed around the nesting tree before dawn. Before sunrise we approached the colony and flushed the birds into the nets. A small number of birds usually managed to escape (by flying over the nets), but the capture success was usually above 80%. The birds were removed from the nets, placed individually in linen bags, and processed. The duration of the procedure depended on the size of the colony but usually lasted 1-3 h. The birds were ringed with a unique numbered ring from the South African Bird Ringing Unit (SAFRING), and in recent years with an additional individual colour combination. Juvenile weavers moult into adult plumage when they are approximately four months old and, before that, their age can be estimated through the development of the black patch on the face and throat (Maclean 1973c; R. Covas, unpubl. data). We considered two age classes: juvenile (younger than 4 months) and adults (fully developed patch, older than 4 months).

During the first five years of the study, the breeding activity of the birds was not directly monitored. In order to determine when the breeding season took place, we used the development of the black patch of juveniles caught to estimate the month of hatching. Information on the presence/absence of brood patches also provided an indication of the breeding season. In total we considered 8 breeding periods (there was no breeding activity in the summer of 1994-1995, and no capture effort during June 1997-May 1998): August 1993 (beginning of the study), October 1993- April 1994, October 1995- April 1996, October 1996- March 1997, October 1997- December 1998, September 1999- May 2000, September 2000- January 2001.

Statistical methods

Estimation of annual survival probabilities and tests for significant differences between different classes of birds were obtained using the general methods of Lebreton *et al.* (1992). Program MARK (Cooch & White 1998; White & Burnham 1999) was used to generate maximum-likelihood estimates of survival and recapture probabilities. MARK is a software package that computes survival and recapture parameters using an information matrix derived from recapture histories, and by

testing the fit of different statistical models, it provides a way to test biological hypotheses (Lebreton *et al.* 1992).

The general notation used was that of Lebreton *et al.* (1992), in which annual survival probability is denoted ϕ and recapture probability, p. Subscripts indicate whether parameters in a model are time-dependent (e.g., ϕ_t, p_t), vary with age (and if so, with how many age classes, e.g., ϕ_{a2}, p_{a2t}), are constant over time (e.g., ϕ, p), are group-specific (e.g., ϕ_g, p_g), or are group- and time-specific (e.g., ϕ_{gt}, p_t). A goodness-of-fit (GOF) test was used to assess the overall fit to the dataset of the model that best explained the weaver data (Lebreton et al. 1992). GOF was assessed using the bootstrapped GOF test in MARK (Cooch & White 1998). This procedure creates a simulated data set based on the model being tested, using the parameter values estimated by the model from the actual data. The simulated data set exactly meets the assumptions inherent in the general capture-mark-recapture framework (no overdispersion, no predominance of transients, etc). The simulated recapture histories are used in a bootstrapping procedure to generate a distribution of model deviances, to which the model deviance for the actual data set is compared.

Different models were tested with the Akaike Information Criterion (AIC; Akaike 1973; Lebreton *et al.* 1992; Burnham & Anderson 1998). MARK provides a calculated AIC value for each model, and those with the lowest values are the most parsimonious. The AIC is used to select among different models; the currently accepted convention (Burnham & Anderson 1998) is that models with AIC that differ by 2 or less are indistinguishable statistically. In general, for model selection and hypothesis testing, the criteria used relied on "AIC weights", a measure of a model's relative probability of being the best model for the data, compared to alternative models (Burnham & Anderson 1998).

Potential differences in survival among different groups of birds were assessed by comparing different models, some of which modelled the effect of the separate groups while others considered the groups identical. If a model with a group effect provided a better fit (as judged by the AIC values and weights) than one without it,

survival was considered to differ among the groups. If, however, a group-effect model did not provide a better fit, the more parsimonious model without a group-effect (with fewer parameters) was used to infer no difference among the groups. The results presented in the tables are not those of all the models tried, but only the 6- 10 models with the lowest AIC and relevant to the hypotheses being tested. The number of estimable parameters in the models was given by MARK; apparent discrepancies in the number of estimable parameters among structurally identical models fitted using different data sets sometimes resulted from sparseness of data.

Because sociable weavers are unpredictable, aseasonal breeders, the time intervals in between our capture occasions were not constant (see above). MARK allows analysis of unequal time intervals between successive capture occasions; for the eight capture occasions, corresponding to the eight breeding periods that occurred between July 1993 and January 2001, we used seven time intervals of 0.67, 2, 0.92, 1.2, 0.58, 1.4, and 0.67 years, respectively. Each interval was defined as the time from the start of the non-breeding period until the end of the successive breeding period. However, all survival and recapture probabilities reported here are annualised ones, that is, for a 12-month period, allowing comparison with other studies. Although some birds were caught during non-breeding periods, these captures were not used in constructing individual encounter histories; a bird had to be caught during a breeding period to be designated as surviving to that period. Total summer rainfall (October-March), and minimum and average winter temperature (May-August) were modelled as constraints on survival. Winter temperature was chosen because passerines are vulnerable to food shortage and climatic severity during winter (e.g. Newton 1998). Weather data were obtained from the Weather Bureau, Pretoria.

RESULTS

Effect of time

Using the entire data set (N = 1486), there was no effect of time period per se on survival probabilities; the four models with the lowest AIC values (models 1–4; Table

1) had no time-dependence. Recapture probabilities did vary with time, however (Table 1); models with constant recapture probabilities had substantively worse fit. This is consistent with the fact that our field effort varied between different time periods. The best-fitting general model, ϕ_{m+m2}, p_t (model 1; Table 1), that incorporated an effect of temperature (see below) met the GOF assumptions for the dataset structure, with the MARK bootstrap procedure showing that the probability of seeing a deviance as large or larger than the observed value from the simulated data was 0.11. Model 4 (Table 1) was used to derive the average annual survival probability using the total data set (N = 1486), which yielded an annual survival probability of 0.662 (± 0.012) for sociable weavers in the Kimberley population.

Effects of winter temperature and rainfall

There was evidence of a winter temperature effect. The two models that constrained survival to be a linear and quadratic function of minimum winter temperature (models 1–2, Table 3.1) were the best models for our data set. Model 1 suggested that survival varied in a curvilinear way with average minimum temperature in winter, being about three times more plausible (based on AIC weights) than the next closest model that included minimum winter temperature as a linear constraint (model 2, Table 3.1). From model 1, the survival estimates in relation to temperature (Fig. 3.1) show that survival increased with increasing temperature in winter over the 2.5–3.5° C. range but declined during the warmest winter. This relationship seemed to be driven primarily by the single winter that was unusually warm; in the remaining years there was an approximately linear increase in survival with minimum winter temperature (Fig. 3.1), reflected in the fact that the linear-constraint model (model 2, Table 3.1) was one of the better fitting ones. The regression coefficient for that model was 0.1553 (± 0.1397). Average winter temperature was not as good a predictor of survival as minimum temperature (Table 3.1), suggesting perhaps that weavers are likely to be more sensitive to cold overnight conditions than to daytime ambient temperatures.

Any effect of rainfall was rejected based on the high AIC values for the models that incorporated rainfall as a constraint on survival (models 8, 10, Table 3.1).

Effects of age

Using only birds of known-age (first caught as juveniles, $N = 471$), there was no effect of age on survival probabilities. The models used included two age classes in which first-year survival was treated as distinct from survival of all older age classes. Model ϕ, p_t (model 11, Table 3.2) provided the best fit; the most closely similar model with the two age classes had a AIC_c that was higher by 5 (model 12; Table 3.2). The model without an age effect was over 13 times more likely based on the AIC weights. Thus, there was little evidence that first-year survival probabilities of sociable weavers differed from that of older birds. The subset of data (known-age birds) used for the age analysis also met the GOF assumptions; the probability of obtaining a deviance as large or larger than that observed was 0.35 for model ϕ, p_t. Using only the known-age birds, model ϕ, p_t estimated average ($\pm$SE) annual survival probability of sociable weavers as 0.659 ($\pm$ 0.021), similar to the estimate from the total dataset.

DISCUSSION

Adult and juvenile survival

As predicted from the latitudinal trend in life histories, we found relatively high adult and juvenile survival. The annual survival estimate obtained for our population was higher than estimates for northern temperate (European) populations of similar sized passerines, which are often around or below 0.5 (see Sæther 1989; Peach *et al.* 2001).

The most unusual result of this study was the finding that juvenile survival was the same as that of adults. In textbooks, juvenile survival is described as being typically half the adult survival rate (e.g. Gill 1995), although this most likely reflects a relatively poor knowledge of juvenile survival and a bias towards north-temperate systems. Post-fledging survival at low latitudes is not well studied and, to our knowledge, this is the first study to report annual survival rates of a juvenile passerine

estimated by capture-recapture methods, so comparisons to other southern species are difficult. Still, some estimates based on re-sighting suggest juvenile survival might be high in the south (e.g. Rowley & Russell 1991; Stacey & Koenig 1990).

The relatively high juvenile survival rate reported here might be related to prolonged parental care and delayed dispersal. In sociable weavers, the parents and/or helpers can feed the young for up to six weeks after fledging. This might have survival value, if it reduces the risks taken during the development of foraging skills (Langen 2000). Still, work on juncos *Junco phaenotus* (Sullivan 1989) showed that mortality of young mainly takes place in the first week after fledging, in which case a few extra weeks of parental feeding might not be able to account for large differences in juvenile survival.

Delayed dispersal has been shown to promote juvenile survival in Siberian jays *Perisoreus infaustus* (Ekman *et al.* 2000) and brown thornbills *Acanthiza pusilla* (Green & Cockburn 2001). In sociable weavers, delayed dispersal is generalised: young never leave the natal colony in their first four months and seldom do so in their first year (Chapter 2). Spending this period in the company of the parents or helpers, and roosting with them in the nest chamber, is likely to provide extra protection from potential sources of mortality such as predators and cold nights. This prolonged parental care and delayed dispersal sharply contrasts with most northern temperate situations, where young generally associate with parents for less than a month (Russell 2000). It is therefore possible that differences in timing of dispersal might account for some of the latitudinal variation in juvenile survival. Additionally, young are expected to also benefit from the other extrinsic factor that also cause low mortality in adults (see below).

Inter-annual survival

The models that best fitted our data had no time-dependence, indicating that year per se had no effect on survival in this population. Temporal variation in survival of passerines seems a relatively common characteristic of northern temperate populations (Newton 1998). This variation is most commonly attributed to changes in

environmental conditions (during or outside the breeding season), leading to fluctuation in food levels, exposure to bad weather, or density-dependent mechanisms. In this study we found evidence of an effect of winter temperature (discussed below). Still, the lack of a random time effect in sociable weavers is interesting because the study period encompassed considerable variation of reproductive effort. Specifically, it included great variation in the duration of the breeding periods — from one year when no breeding activity was detected to a continuous 9-month breeding season — yet this was not reflected in survival. The evolution of avian life histories has often been linked to variation in food availability. Where food levels are low, birds should reduce reproductive effort, which would lead to high survival through a decrease in the cost of reproduction (Lack 1968; Martin 1987; Stearns 1992). If survival in sociable weavers was determined mainly by variation in fecundity, a time effect should have been detected. Failure in finding it suggests that intrinsic factors alone (i.e., as a direct result of reproductive effort) cannot explain survival in this species. Of course, a problem with correlational studies such as this one, is that the probability of detecting reproductive costs based on natural variation is low if individuals adjust reproductive effort to environmental conditions. Still, our results suggest that, even if individuals adjust reproductive effort, they seem to do so without compromising survival, which is consistent with the view that life histories at low latitudes are mainly driven by high extrinsic survival (Martin 2002).

Environmental factors

Survival in this study increased with minimum winter temperature, but decreased in the warmest year. Differences in winter conditions have been invoked to explain differences in survival rates at different latitudes (Rowley & Russell 1991; Ghalambor & Martin 2001). A severe winter might decrease survival of bird populations in at least three ways: (1) through decreased foraging opportunities (e.g. persistent snow or rain; Cuthill & Houston 1997); (2) through decreased food availability (Jansson *et al.* 1981; Brittingham & Temple 1988; Newton 1998); or (3) through higher energetic demands for thermoregulation (Macnamara & Houston 1990; Cuthill & Houston

1997). Sociable weavers inhabit an area where winter days are usually sunny with temperatures above 15°. Under such conditions an effect of bad weather on foraging opportunities should be negligible. Variations in winter temperature are also unlikely to play a significant role in limiting food availability in the study area. In the Kalahari, one of the main food sources for sociable weavers, and many other species, is the harvester termite *Hodotermes mossambicus* (Maclean 1973d), which increases its daily activity in winter, when the temperatures are cooler (R. Adam, pers. comm.; Richardson 1985). Availability of other insects during winter is low, regardless of variations in temperature; in these areas insects emerge from spring through summer, with the major emergence being dependent on rainfall (M. Picker, pers. comm.).

Winter temperatures, however, might affect survival in sociable weavers through increased energetic demands for thermoregulation. In the study area, winter temperatures at night can drop to -8°. The sociable weaver nest mass and the habit of communal roosting likely help the weavers cope with cold night-time temperatures. White *et al.* (1975) have shown that the relatively high temperatures in the nest chambers during the night diminish the metabolic cost of thermoregulation, allowing an energy expenditure of about 40% less than if the birds roosted in the open. However, survival costs associated with low winter temperatures and nocturnal thermoregulation can still occur, as was found in a southern-temperate population of the group-living red-billed woodhoopoe (*Phoeniculus purpureus*; du Plessis & Williams 1994). The decline in survival observed in the warmest year is surprising. It has been shown that, above a certain temperature, there might be costs associated with energetic demands of thermoregulation, since birds huddling in a chamber may spend considerably more energy than non-huddling birds (Boix-Hinzen & Lovegrove 1998). However, this study was conducted in summer when night-time temperatures were considerably warmer than those experienced in the warmest winter in our area. This decline in survival could also be an artefact of some other factor with a negative effect of survival, such as increased reproductive effort or low food availability. Still, the low survival winter took place after a relatively dry summer, when reproductive effort

was low. Alternatively, it could have been a consequence of bad conditions with low food levels, but we found no effect of rainfall on survival.

The fact that rainfall did not affect survival in this population was surprising, since rainfall, through its effect on insect abundance and production of seeds, is believed to be the main determinant of food availability in these semi-arid regions (Maclean 1973c; Harrison *et al.* 1997; Lloyd 1999; Dean & Milton 2001). Thus, our results contrast with studies on northern temperate birds, where food availability has been shown to influence survival in birds (Jansson *et al.* 1981; Brittingham & Temple 1988; Newton 1998). The absence of a rainfall effect suggests that, although food levels can vary greatly in this region, the lowest levels experienced in winter are always higher than those experienced by northern temperate birds. This is consistent with the fact that harvester termites increase their activity in winter (see above). Moreover, in this region the seed bank does not become exhausted under normal circumstances (A. van Rooyen pers. comm.). Relatively high food levels outside the breeding season have been suggested to be responsible for high adult survival of birds in southern Africa (Peach *et al.* 2001) and Australia (Ford *et al.* 1988; Rowley & Russell 1991) and for the latitudinal trend at a global scale (Ricklefs 1980).

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TABLES

Table 3.1. Models to assess the effect of time period ($_t$), minimum ($_m$) and average ($_v$) winter temperature and rainfall ($_r$) on survival and recapture probabilities in sociable weavers, using all data (N = 1486 birds).

Model	AIC	AIC weight	Number of estimable parameters	Deviance
(1) ϕ_{m+m2}, p_t	2930.8	0.4813	9	106.0
(2) ϕ_m, p_t	2933.0	0.1585	8	110.2
(3) ϕ_v, p_t	2934.0	0.0955	8	111.2
(4) ϕ, p_t	2934.2	0.0847	8	111.5
(5) ϕ_t, p_t	2935.0	0.0589	12	104.1
(6) ϕ_{m*t}, p_t	2935.0	0.0589	12	104.1
(7) ϕ_{v*t}, p_t	2935.0	0.0589	12	104.1
(8) ϕ_{r*t}, p	2940.8	0.0032	11	112.0
(9) ϕ, p	3472.4	0.0000	2	661.7
(10) ϕ_r, p_t	3552.3	0.0000	7	731.6

Table 3.2. Models to assess the effect of age on survival and recapture probabilities in sociable weavers. The age classes used were the first year and all older ages combined (N = 471 birds).

Model	AIC	AIC weight	Number of estimable parameters	Deviance
(11) ϕ, p_t	963.8	0.9033	8	74.4
(12) ϕ_t, p_t	968.9	0.0688	12	71.2
(13) ϕ_{a2}, p_t	970.8	0.0277	8	81.3
(14) ϕ_{a2t}, p_t	981.2	0.0002	13	81.4
(15) ϕ_t, p	1059.5	0.0000	8	170.0
(16) ϕ, p	1116.0	0.0000	2	238.8

FIGURES

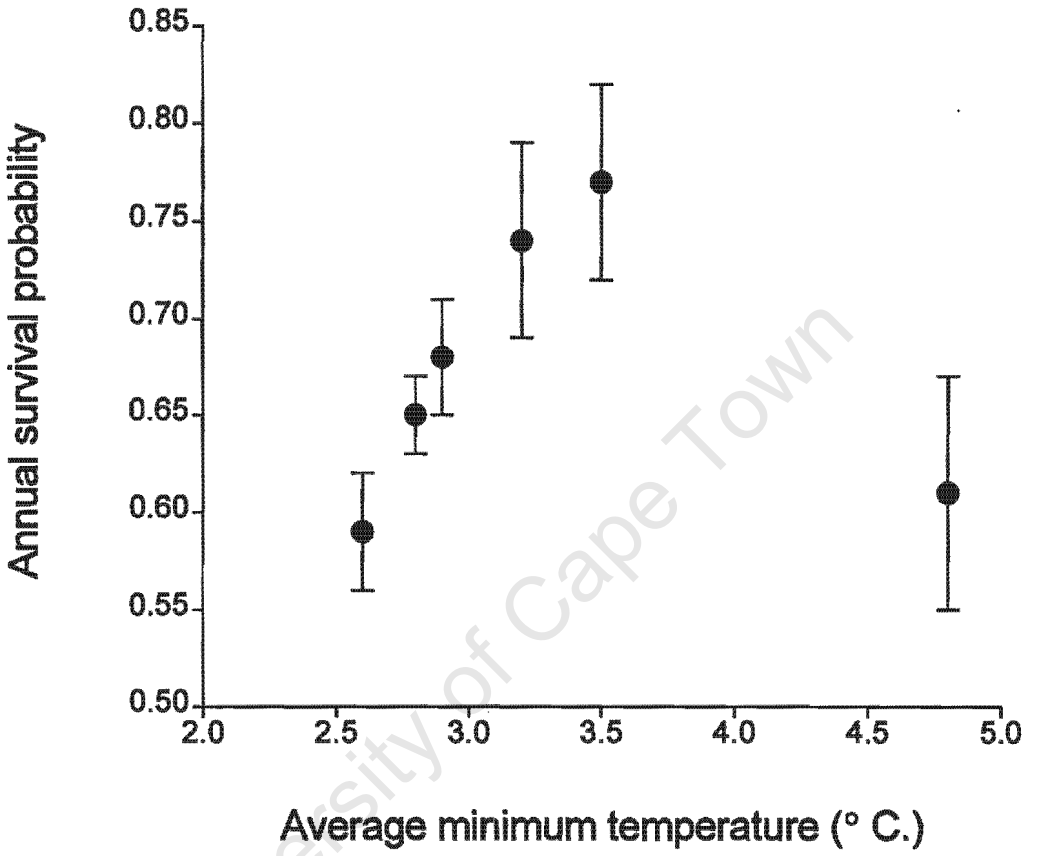

Fig. 3.1 – Annual survival estimates of sociable weavers in relation to average minimum winter temperature (N=1486 birds). Parameter estimates and 95% confidence intervals are shown.

4

STABILISING SELECTION ON BODY MASS IN THE SOCIABLE WEAVER

Until recently, survival of small passerines was believed to increase with increasing body mass despite some evidence that birds with high fat levels might incur a survival cost due to impaired flight speed and manoeuvrability that make them less efficient at escaping avian predators. In this study an 8-year data set is used to investigate survival in relation to body mass in a wild population of sociable weavers (*Philetairus socius*), a savannah dwelling passerine. We present evidence for strong stabilising selection on body mass, verifying the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass. This pattern in survival stemmed from an effect of body mass *per se*, as the results could not be explained by skeletal body size (as measured by tarsus length) or condition in relation to body size.

INTRODUCTION

Survival is a key life history trait in ecological and evolutionary theory, so it is important to know the factors that might affect it and how. Among birds, body mass is one of the factors that can influence survival, with the common assumption being that post-fledging survival increases with body mass at fledging (e.g Perrins 1965; Gill 1995; Brown & Brown 1996). It is also believed that low body mass can reduce adult survival, for example, through an increase in the risk of starvation (Rogers & Smith 1993; Cuthill & Houston 1997) or the weakened immunocompetence of lighter birds (Møller et al. 1998). However, there are also costs associated with high body mass, stemming mostly from the disadvantages of carrying high fat levels (Lima 1986; Witter & Cuthill 1993; Cuthill & Houston 1997). These costs are usually expressed in terms of predation risk, either through increased foraging time and thus increased exposure or through decreased flight manoeuvrability (Lima 1986; Witter & Cuthill 1993; Cuthill & Houston 1997). An important question, however, is not whether high body mass has costs, but whether they are of sufficient magnitude to be biologically interesting (Cuthill & Houston 1997). If both low and high body mass have significant costs, survival of both relatively lean and fat individuals should decrease, resulting in stabilising selection on body mass (see also Endler 1986; Adriaensen et al. 1998). Several studies have investigated possible costs of high body mass (e.g. Metcalfe & Ure 1995; Kullberg et al. 1996; Gosler et al. 1995), although the link between high body mass and survival was indirect. An exception was a study on blue tits *Parus caeruleus*, in which Adriaensen et al. (1998) found that high fledgling body mass had a negative effect on survival in the presence of an avian predator but not in its absence.

In this study we use a long-term data set to investigate the relationship between mass and survival in adult and juvenile sociable weavers *Philetairus socius*, a sedentary group-living passerine endemic to the arid savannahs of southern Africa. Because body mass is related to skeletal body size and condition, we also examine how these two variables affect survival. We present evidence for strong stabilising selection on

body mass, and thus verify the prediction that body mass represents a trade-off between the benefits of storing fat to avoid starvation and the benefits of losing mass possibly to avoid predation.

METHODS

Study area and species

The sociable weaver is a colonial, cooperatively breeding passerine endemic to southern Africa (Maclean 1973a,c; Mendelsohn & Anderson 1997). Sociable weavers weigh approximately 26-32 g (mean 28.7 g), with the sexes being indistinguishable in the field. There are no significant inter-sexual differences in mass, but males have a significantly longer tarsus than females (23.65mm ± 0.56 vs. 23.44mm ± 0.53; t= 2.61, d.f.= 185, p= 0.01). Sociable weavers feed predominantly on insects (80% of their diet), seeds and other plant products, and forage predominately on the ground but also on the bark and leaves of trees (Maclean 1973d). The weavers build a very large communal nest with separate chambers in which they roost and breed. The nest is usually built on *Acacia erioloba* trees, but other structures may be used (Maclean 1973a). The nest mass is maintained and occupied by the whole colony throughout the year. At night the birds roost in the chambers within the nest mass, and may also return to the nest during the day to escape predators (pers. obs.) or to seek protection from high daytime temperatures (Maclean 1973d). The start of the aseasonal breeding period is usually triggered by rainfall, which is also a major determinant of the duration of the nesting period, number of broods raised (1-8) and clutch size laid (2-6; Maclean 1973b; Chapter 2).

The study took place at Benfontein Game Farm, near Kimberley, in the Northern Cape Province, South Africa (approx. 28°53'S 24°49'E). The vegetation consists of semi-arid open savannah and is dominated by *Stipagrostis* grasses and the camelthorn tree *A. erioloba*. The area is semi-arid, experiencing low and unpredictable rainfall (average 431±127 mm per year; Weather Bureau, Pretoria), with most of the precipitation falling during summer. The daily temperature ranges are typically high,

with cool/warm nights and hot days in summer (approx. 8-40°C) and very cold nights and mild days in winter (approx. -8-25°C).

Field methods

A capture-mark-recapture study at Benfontein was conducted from August 1993 to November 2000. The study area contained 24 sociable weaver colonies; at 15-20 colonies the birds were captured twice a year. During the first five years the capture effort was constant throughout the year (i.e. 1-2 colonies caught every month). From mid-1998 until the end of the study we concentrated capture efforts on the 1-2 consecutive months at the beginning and end of the breeding period. The birds were captured with mist nets, which were placed around the nesting tree before dawn. Generally, 70-100% of the colony residents were caught. The birds were individually ringed with a numbered metal ring (from SAFRING, University of Cape Town). We measured mass (to the nearest 0.5 g), and tarsus (to the nearest 0.1 mm; only measured regularly in the last three years of the study). The age of juvenile weavers was estimated through the development of the black patch on the face and throat (Maclean 1973b). Upon capture, birds were designated as adults if older than 120 days, otherwise as juveniles.

Statistical methods

Annual survival probabilities were estimated and tested for significant differences between different classes of birds using the general methods of Lebreton *et al* (1992). Program MARK (Cooch & White 1998; White & Burnham 1999) was used to generate maximum-likelihood estimates of survival and recapture probabilities. MARK is a software package that computes survival, recapture, and movement parameters using an information matrix derived from recapture histories. It provides a powerful way of testing the fit of different statistical models and thus tests different biological hypotheses (Lebreton *et al.* 1992). The general notation used is that of Lebreton *et al.* (1992), in which annual survival probability is denoted ϕ and recapture probability, p. Subscripts indicate whether a model incorporates time-dependence in a

parameter estimate (e.g., ϕ_t, p_t), an effect of age (and if so, how many age classes, e.g., ϕ_{a2}, p_{a2t}), constancy over time (e.g., ϕ, p), or an effect of a co-variate (e.g., ϕ_c, p_g).

A goodness-of-fit (GOF) test, was used to assess the overall fit of the data-set to the most general Cormack-Jolly-Seber (CJS) model that best explained the weaver data (Lebreton *et al.* 1992). From that, a variety of more biologically relevant models were tested, incorporating various combinations of age-, co-variate-, and time-dependence. GOF was assessed using the bootstrapped GOF test in MARK (Cooch & White 1998). This procedure creates a simulated data set based on the model being tested, using the parameter values estimated by the model from the actual data. The simulated data set exactly meets the assumptions inherent in the general capture-mark-recapture framework (no overdispersion, no predominance of transients, etc). The simulated recapture histories are used in a bootstrapping procedure to generate a distribution of model deviances (below), to which the model deviance for the actual data set is compared. Using the bootstrapped GOF test it was found that the sociable weavers data met the general CJS assumptions ($p = 0.29$).

Testing and selection among different models was done by examining their Akaike Information Criterion (AIC; Akaike 1973) values (Lebreton *et al.* 1992; Burnham and Anderson 1998). MARK provides calculated AIC values corrected for over-dispersion in the data (AIC_c). Models with the lowest values of AIC_c are the most parsimonious. The currently accepted convention is that models with AIC_c that differ by less than 2 are indistinguishable statistically (Burnham & Anderson 1998). In these cases, other criteria (likelihood ratio test, number of parameters, intuition) should be used to accept or reject the different models. The results presented in the tables include only the 3–5 models with the lowest AIC_c and relevant to the hypotheses being tested. The number of estimable parameters in the models was given by MARK; apparent discrepancies in the number of estimable parameters among models sometimes resulted from sparseness of data for certain parameters, making them inestimable for that reason.

Because sociable weavers are unpredictable, aseasonal breeders, the time intervals between capture occasions were not constant. MARK allows analysis of unequal time intervals between successive capture occasions. For the eight capture occasions, corresponding to the eight breeding periods that occurred between July 1993 and January 2001, we used seven time intervals of 0.67, 2, 0.92, 1.2, 0.58, 1.4, and 0.67 years, respectively. Each interval was defined as the time from the start of the non-breeding period until the end of the successive breeding period. Although some birds were caught during non-breeding periods, these captures were not used in constructing individual encounter histories; a bird had to be caught during a breeding period to be designated as surviving to that period. Co-variates, used were body mass in grams, taken each time a bird was captured and averaged over all captures for individuals caught multiple times; and tarsus length, usually measured once for each individual. Because mass might co-vary with skeletal body size, a model with a condition index (mass/tarsus) was also included. These variables were used as continuous co-variates, and models constructed constrained survival to be a function of each. Whenever there was an apparent linear relationship with a given variable, it was also tested whether there were higher-order (i.e., non-linear) relationships with that co-variate.

RESULTS

Juvenile mass was related to survival in a non-linear way. A model incorporating mass and mass^2 as co-variates (model 2; Table 4.1) was a better fit than models with solely mass or without a mass effect, using the sample of birds first banded and weighed as juveniles (N = 435). There was no improvement by using a model with age-dependent survival, consistent with other analyses showing no age-related effects on survival (Chapter 3). This indicates that the apparent effect of juvenile mass is expressed across age classes and is not confined only to the juvenile's first year of life (and is consistent with the similar results for adult body mass; see below). The best-fitting and most parsimonious model 2 (Table 4.1) yielded a regression equation

describing a curvilinear relationship between juvenile mass and survival plotted in Fig. 4.1a over the observed range of juvenile masses. This illustrates a strong disadvantage for birds lighter or heavier than the mean, and suggests a high level of stabilising selection on body mass.

A similar relationship with adult body mass was found. Using all birds for which we had body masses measured as adults (and using an average value for each bird weighed multiple times; N = 977), a model with survival constrained as a function of mass + mass^2 provided the best fit (model 6; Table 4.2). In the case of adults, this non-linear relationship was statistically much stronger than in the juveniles (as illustrated by the AIC_c values; Table 4.2), although the pattern was the same (Fig. 4.1). For neither adults nor juveniles was there any time-dependent effect of body mass on survival (Tables 4.1, 4.2), suggesting that this curvilinear relationship held across years. The regression equation predicted by model 6 described a strong effect of adult mass on survival over the range of observed mass values (Fig. 4.1b). As in juveniles, there appeared to be strong stabilising selection on adult body mass.

Overall skeletal size, as reflected in tarsus length, was also related to survival probability in sociable weavers. For this analysis only birds initially banded during the final three breeding periods were used (N = 318). This was because tarsus was not routinely measured on birds in the earlier years of the study. To avoid bias by potentially including a non-random sample of unusually old birds, any individual first banded in an earlier season and then caught and its tarsus measured during the final three breeding periods was not included. Over this more limited time frame, a model with tarsus as a continuous co-variate provided the best fit (model 11; Table 4.3). Unlike with mass, there was no evidence for strong higher-order effects of tarsus length; a model with tarsus + tarsus^2 (model 12; Table 4.3) did not provide a better fit. The relationship predicted by model 11 shows a marked increase in survival probability with tarsus length over the range of tarsus lengths observed in the population (Fig. 4.2). Thus, weavers with large skeletal body size — but of average mass — are apparently favoured.

Finally, using the same data set as that used for analysing tarsus length, condition (as measured by mass/tarsus length) had no apparent effect on survival. A model with condition as a continuous co-variate, ϕ_{cn}, p_t, yielded an AIC_c of 317.3, compared to one without condition as a co-variate, ϕ, p_t, with an AIC_c of 318.5. This might be due to the fact that tarsus is a poor predictor of mass in this species, even if males and females are taken separately (overall: $r^2 = 0.09$; Males: $r^2 = 0.14$; females $r^2 = 0.04$).

DISCUSSION

This study showed a strong disadvantage for birds lighter or heavier than the mean, suggesting stabilising selection on body mass. To my knowledge, this is the first long-term study on a natural population showing such an effect on both adult and juvenile birds. It is often assumed that increasing body mass should result in increasing survival. Yet, there is growing evidence that high mass is not always advantageous, because an increase in fat reserves may lead to impaired flight performance and compromise one's escape from predators. However, no one has previously demonstrated a survival cost of high mass. This result was obtained in a non-migrant, non-fat-storing species, which shows that even moderate variations in body mass (i.e., 10-20% around the mean) can have a significant effect on survival.

This result was due to body mass and not to a confounding effect of skeletal body size, since in our population survival increased linearly with body size (measured as tarsus). Increased survival with increasing body size might reflect enhanced survival in males, which are slightly larger than females. This seems to be a common pattern in other bird species (Breitwisch 1989). However, because there are no significant differences between male and female body mass of sociable weavers, the results are not affected by sex. We found no effect of body condition on survival, which might be due to the fact that tarsus is a poor predictor of body condition in this species (see above). Furthermore, the condition analyses were based on a much smaller subset of the data.

The finding of increased mortality at high body mass levels could also be an artefact of heavier birds having greater propensity for dispersal. This, however, is unlikely. Sociable weavers are highly sedentary, and only 6% of the birds ringed were recaptured at other colonies. Moreover, 15-20 colonies out of 24 were monitored, and thus a considerable proportion of the birds that dispersed was recaptured. There were also no differences in mass between philopatric birds and those that dispersed.

In general, light birds with low fat reserves face higher risk of starvation due to unpredictability of foraging success (Lima 1986; Rogers & Smith 1993; Cuthill & Houston 1997). For example, birds at high latitudes can experience long cold nights or snow storms that make food inaccessible. However, it has been shown that in habitats where foraging predictability is high – and hence the survivorship benefits of high body mass are reduced, while the survivorship costs of high body mass are maintained – birds should be leaner than those facing high foraging unpredictability (Rogers & Smith 1993). The species studied here inhabits an area where climate is relatively mild and prolonged bad weather is rare, particularly in winter, when the days are normally sunny with warm temperatures. Cold nights often occur in winter, but sociable weavers partially cope with the energy demands of cold weather through roosting in the communal nest structure and by huddling (White *et al.* 1975). Still, it seems likely that part of that energy demand will be supplied by body reserves, such that birds with low fat reserves incur a cost, especially whenever cold weather lasts several days (e.g. Brown & Brown 1998). Low fat reserves might also reflect disease, high parasite loads (Brown & Brown 1996, Marsden 1999) or weakened immune function (Møller *et al.* 1998), all of which may negatively affect survival.

Body mass should result mainly from a trade-off between storing mass for energy and shedding mass to avoid predation (Lima 1986, Witter & Cuthill 1993, Cuthill & Houston 1997). A limit on high body mass should exist because leaner birds are more agile in escaping predators, and they spend less time feeding, thus being exposed to predation for shorter periods. Several studies of captive birds have investigated agility, showing that fatter birds have lower take-off speed and manoeuvrability (e.g., Metcalfe & Ure 1995, Kullberg *et al.* 1996), but no direct

relation to predation probabilities or mortality has been established. Others have questioned whether such impaired flight performance could have much effect, since under a true predation threat, birds are expected to use their maximum power (e.g. Kullberg 1998; Veasey *et al.* 1998). Studies in the wild have found indirect evidence for a trade-off between body mass and predation risk. For example, Gosler *et al.* (1995) found that great tits *Parus major* became significantly heavier when sparrowhawks *Accipiter nisus* were absent from the area due to pesticide poisoning, and became lighter when the hawks re-occupied the area. To my knowledge, the only study directly linking body mass to survival was that of Adriaensen *et al.* (1998), who showed that the shape of the curve describing fledgling survival as a function of body mass changed from a monotonically increasing relationship in predator-free plots to a curve with an optimum around the mean in the presence of sparrowhawks. The present study also found impaired survival at low and high body mass, but in this case this held across all years of the study (since there was no time-dependent effect of mass on survival). The same trend in both age classes was expected since, in this sedentary species, juvenile birds are subjected to the same factors that affect mass and survival in adults (see also Adriaensen *et al.* 1998); furthermore, survival is not age-dependent in the sociable weaver (Chapter 3). Like some of the results of Adriaensen *et al.* (1998) on blue tits, these results on sociable weavers contradict the often accepted view that survival always increases with mass.

Predation most likely explains why heavier birds had higher mortality in this study, since sociable weavers inhabit open savannah areas where predation by raptors in general is probably high (Du Plessis *et al.* 1995). Furthermore, predation by the Gabar goshawk *Micronisus gabar* is known to be important in this species (Maclean 1973c; Marsden 1999), and in the study area (R. Covas and M.D. Anderson, pers. obs.). Avian predators usually attack sociable weavers while they are foraging on open ground, or moving between trees; to escape the predator, weavers fly to the nearest tree or to the colony, hiding inside the nests when possible (pers. obs.). Thus manoeuvrability and flight speed are likely to be critical for sociable weaver survival.

In conclusion, we verified the theoretical prediction that the costs of both low and high mass should lead to stabilising selection for intermediate mass, and this trade-off likely leads to the masses observed in the field.

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TABLES

Table 4.1. Models to assess the effect of juvenile body mass on survival probabilities in sociable weavers. Mass was a continuous co-variate, and some models incorporated both mass (m) and mass^2 (m^2) as predictors. The age classes used were the first year and all older ages combined.

Model	AIC_c	Number of estimable parameters	Deviance
(1) $\phi_{m + m2 \cdot a2}, p_t$	916.5	12	891.9
(2) $\phi_{m + m2,}, p_t$	917.0	9	898.6
(3) $\phi_{m + m2 \cdot t}, p_t$	917.6	21	873.8
(4) ϕ_m, p_t	919.4	8	903.1
(5) ϕ, p_t	919.5	8	903.2

Table 4.2. Models to assess the effect of adult body mass on survival probabilities in sociable weavers. Mass was a continuous co-variate, and some models incorporated both mass (m) and mass^2 (m^2) as predictors.

Model	AIC_c	Number of estimable parameters	Deviance
(6) ϕ_{m+m2}, p_t	1921.7	9	1903.6
(7) ϕ_{m+m2*t}, p_t	1926.2	23	1879.3
(8) ϕ_{m*t}, p_t	1929.2	17	1894.7
(9) ϕ_{m}, p_t	1935.0	8	1918.9
(10) ϕ, p_t	1936.0	7	1921.9

Table 4.3. Models to assess the effect of tarsus length on survival probabilities in sociable weavers. Tarsus length was a continuous co-variate, and some models incorporated both tarsus length (ta) and tarsus length^2 (ta^2) as predictors.

Model	AIC_c	Number of estimable parameters	Deviance
(11) ϕ_{ta}, p_t	326.2	3	320.1
(12) $\phi_{ta + ta2,}, p_t$	328.1	4	320.0
(13) ϕ, p_t	331.2	3	325.1

FIGURES

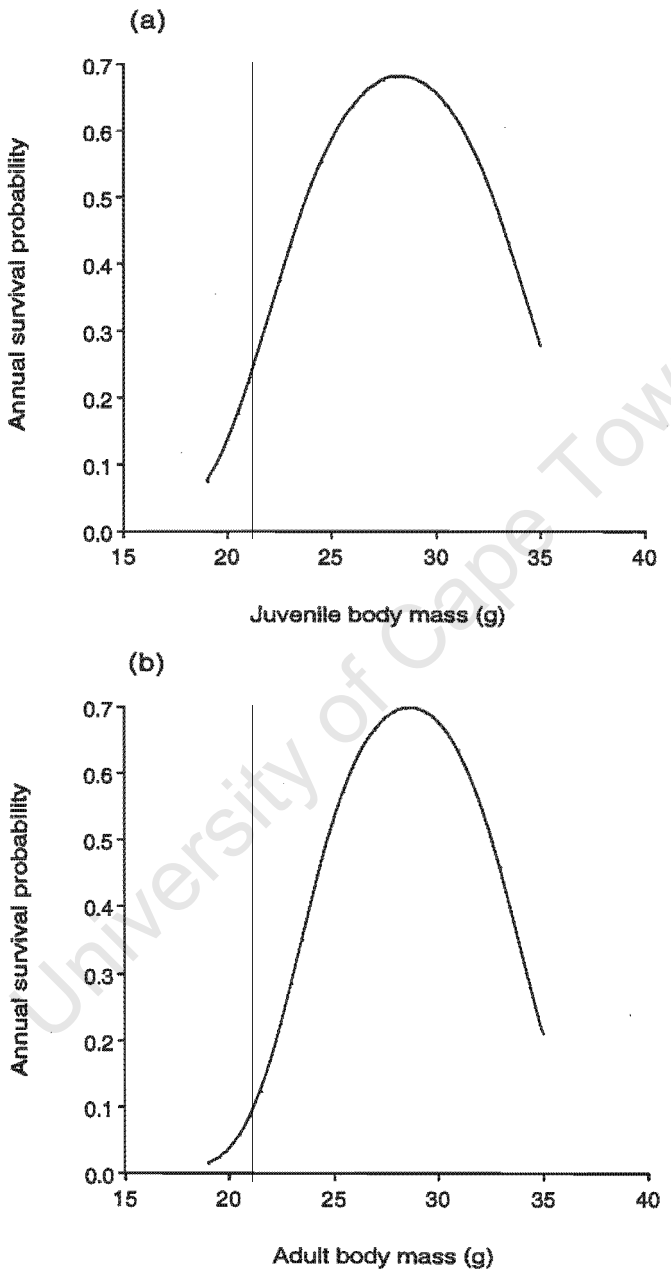

Fig. 4.1. Relationship between body mass and annual survival in sociable weavers as estimated from models (Tables 1, 2) with mass + mass^2 as covariates, for juveniles (a) and adults (b) (Juveniles: 27.9 g ± 2.0, N=435; Adults: 28.7 g ± 2.2, N=977; mean ± SD, N). Note same scale for each.

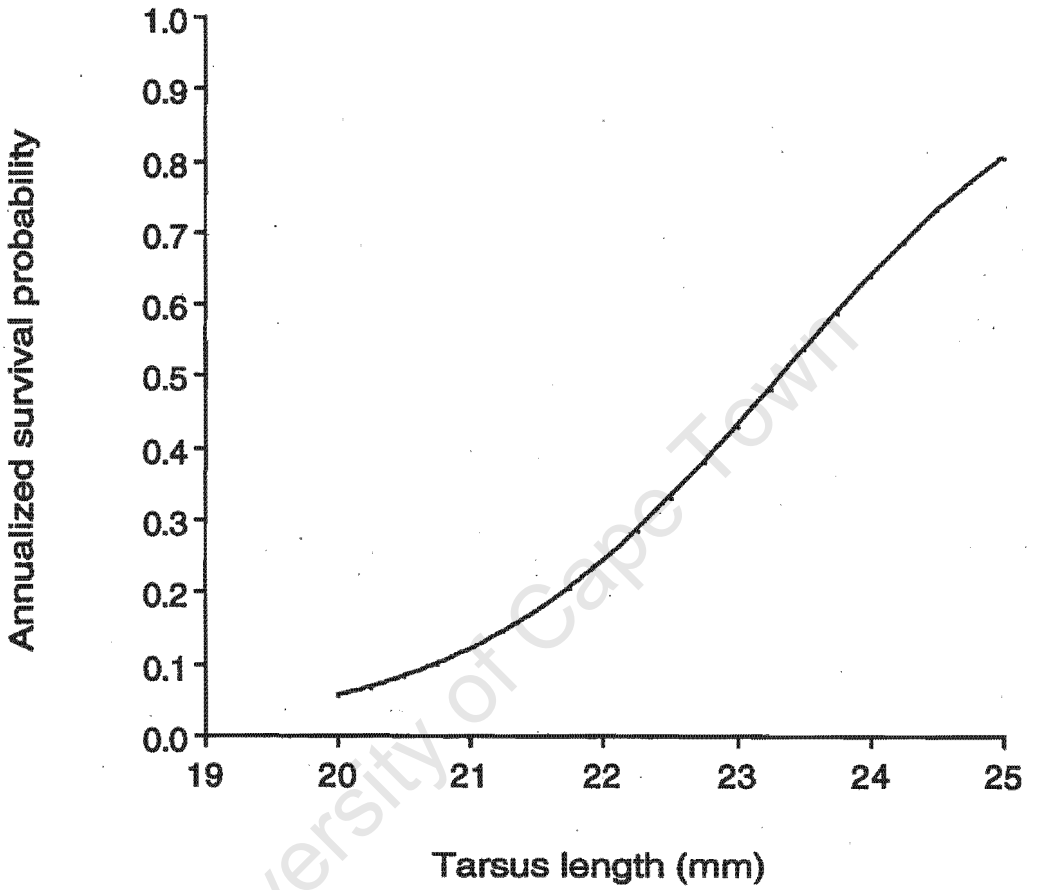

Fig. 4.2. Relationship between tarsus length and annual survival in adult sociable weavers as estimated from a model (Table 3) with tarsus length as a covariate. (23.6 mm ± 0.6, 697; mean ± S.D., N).

5

Brood size manipulations in a southern temperate passerine: no extra effort for extra young

Avian life histories at low latitudes are characterised by high survival and low fecundity. Traditionally, research in avian life history evolution has focused on the evolution of clutch size; yet it has recently been suggested that differences in extrinsic mortality at low latitudes should result in higher survival in the south, which would favour reduced fecundity. According to this view, parents should be reluctant to risk their own survival in favour of current reproduction. This model was tested on a southern temperate passerine, the sociable weaver, by forcing parents to commit themselves to increased reproductive effort through brood size manipulations. Sociable weavers never raised a fully enlarged brood, while fledgling mass did not differ between enlarged broods and controls, suggesting that these birds favour their own survival in preference to that of their young.

INTRODUCTION

Birds have been widely used as models in studies of variation in life history traits (see reviews in Cody 1966; Williams 1966; Lack 1968; Martin 1987). Yet, life history research on birds has been primarily concerned with explaining differences in clutch size at a regional level, thus actually investigating the role of proximate optimisation of fitness and not evolutionary processes (Martin 2002). An interesting challenge for the study of life history evolution in birds is posed by the latitudinal pattern in life histories. When compared to their northern counterparts, birds in the tropics and the southern hemisphere are characterised by lower fecundity, longer parental care periods and higher survival (Martin 1996; Russell 2000; Ghalambor & Martin 2001). This pattern was first identified by Moreau (1944). Since then, different hypotheses have been put forward to explain it, but with no general consensus. Recently Martin (2002) suggested that differences in life histories at different latitudes could be explained by differences in extrinsic mortality rates. Harsher winters in the north should result in higher extrinsic mortality, which, according to theory, should favour increased fecundity. In contrast, higher winter survival in the south should allow longer life expectancies, favouring reduced fecundity. Simultaneously, parents may extend parental care of fewer young, since this should increase reproductive success through higher juvenile survival, while not posing a considerable cost to parents (Russell 2000).

In this study, I investigate whether sociable weavers *Philetairus socius* adopt a different life history strategy from that of northern passerines. To this end, I manipulated sociable weaver broods over two years. Most studies on reproductive effort have been carried out on short-lived north-temperate passerines (Lindén & Møller 1989), where survival prospects are usually so low that an increase in reproductive effort, even at the expense of parental survival, would be expected (Charlesworth 1994). By contrast, relatively long-lived southern-temperate passerines should in theory be less willing to increase reproductive effort (Curio 1988; Woller *et al.* 1992; Charlesworth 1994; but see Erikstad *et al.* 1998). In long-lived species a

decrease in survival would decrease the number of future breeding attempts, thus reducing lifetime reproductive success (Stearns 1992, Charlesworth 1994). Therefore, these species should value their own survival over that of their offspring. Brood size manipulations have rarely been performed at low latitudes (see VanderWerf 1992). Two recent brood size manipulation studies on tropical (house wrens *Troglodytes aedon*; Young 1996) and southern temperate passerines (bell miners *Manorina melanophrys*; Poiani 1993) differed in whether adults worked harder to raise the enlarged brood. In both studies, however, enlarged broods fledged more young than control ones. Other studies of tropical birds have found that parents did not raise enlarged broods (e.g. white-rumped swiftlets *Aerodramus spodiopygius*, Tarburton 1987; snail kites *Rostrhamus sociabilis*, Beissinger 1990).

Sociable weavers are colonial cooperative breeders endemic to the semi-arid savannahs of southern Africa. They are relatively long lived (up to 9+ years) and have an annual survival estimate of 66% (Chapter 3), which is higher than most north temperate Old World passerines of the same size (i.e. approximately 28g; see Sæther 1989; Peach 2001). Parents forced to raise extra young, when compared to control broods may adopt one of the following strategies: 1) work harder to raise the current brood, thereby increasing their parental investment and their chances of suffering a decrease in survival or future fecundity through the trade-off between present and future fecundity; 2) maintain the same levels of investment and fledge young in poorer condition, or fledge fewer young in the same condition as control broods; 3) a combination of these. I predicted that these birds should differentially invest in their own survival rather than that of their young (strategy 2), and should favour offspring quality to quantity. Therefore, an artificial brood enlargement should result in 1) slight or no adjustment of workloads to raise the extra young; 2) high nestling mortality, and 3) no significant differences in fledging mass.

METHODS

Study area and species

The sociable weaver is a small passerine (26-32g) endemic to the arid and semi-arid savannahs of southern Africa (Maclean 1973a; Mendelsohn & Anderson 1997). They feed predominantly on insects, but also on seeds and other plant products (Maclean 1973c). Sociable weavers are colonial, cooperative breeders that build a large communal nest with separate chambers in which pairs and their helpers (consisting of offspring or other birds) roost and breed. The communal nest structure is built on a variety of sturdy structures, but in our study area, the nests are almost exclusively constructed on *Acacia erioloba* trees. Colonies can remain active for several decades, being occupied by successive generations of weavers, all of whom continually add material to the structure.

The study was conducted at Benfontein Game Farm, situated about 6 km south-east of Kimberley, in the Northern Cape Province, South Africa (28°53'S, 24°89'E). The vegetation in the study area consists of open savannah and is dominated by *Stipagrostis* grasses and the camelthorn tree *A. erioloba*. The area is semi-arid, experiencing low and unpredictable rainfall (average 431 $\pm$ 127 mm per year, C.V.= 35.4; Weather Bureau, Pretoria), with most of the precipitation falling during the summer months from September to April.

The study was conducted on a colour-ringed population during two breeding seasons, from Sep 99 - Apr 00 and from Sep 00 - Jan 01. These two seasons experienced contrasting rainfall conditions (the first year had above average rainfall and the second year below average rainfall), resulting in conspicuous differences in both reproductive effort and success (see Chapter 2).

Brood size manipulations

During the breeding season, all nest chambers in each colony were inspected every 4-7 days to detect initiation of new clutches. I used a small round mirror with a torch lamp fitted to it to inspect the contents of each nest chamber. This allowed an accurate determination of the nesting progress. Sociable weaver eggs usually hatch

asynchronously at 1-day intervals, although two or more eggs occasionally hatched in one day. Nests were visited daily near hatching date until hatching was complete. Only nests where hatching started in the same day were used. The day the first egg hatched was day one. I created enlarged broods by removing two 1-3 day-old chicks from the nest assigned to the 'reduced' treatment and adding them to the 'enlarged' treatment. All treatments were randomly chosen using the flip of a coin, although the choice of some nests was constrained by hatching patterns. For example, when hatching happened simultaneously at only two nests and one egg failed to hatch in one of these, this nest could no longer become an enlarged nest, although two chicks from that nest could be used to create an enlarged brood elsewhere. Because hatching is normally asynchronous, there is a size hierarchy in broods and smaller chicks experience higher mortality (unpubl. data). I mimicked this size pattern by always adding a first hatched and a last hatched chick to create the enlarged broods. No enlarged brood ever exceeded the maximum natural brood size in sociable weavers, i.e. six nestlings. Reduced broods were therefore left with one or two intermediate chicks. No broods were ever depleted; i.e., 2-egg clutches were never used as donors. Control broods were created by swapping one first- and one last-hatched chick between two broods without altering the size of those broods.

To collect data on feeding rate and identify all the individuals feeding at a given nest I conducted 1-2 hour observations between 7-10 am for 4 days, when nestlings were 3-6 days old, from under a hide placed 2-5m from the colony. The choice of this period was constrained by nestling mortality, which became fairly high after 6 days. During this period the contents of the nest chambers were inspected daily to verify the number of chicks present. If substantial mortality occurred in a nest during this period (i.e., if 2+ chicks disappeared), this nest was excluded from the analyses of feeding rates. Nests were visited again on day 9, when the number of nestlings was recorded, and on day 17, when all nestlings were weighed and ringed. The nestling period is 21-24 days and the nestlings will usually fledge prematurely if disturbed from day 18 onwards. Therefore, I assumed that the number of chicks present at day 17 was the number of chicks fledged from that nest. Predation is the major cause of nesting

failure in this species (Maclean 1973b; Marsden 1999), with up to 80% of the broods in a season being taken by predators (Chapter 2). The main nest predators are snakes, the boomslang *Dispholidus typus* and the Cape cobra *Naja nivea*, which raid the colonies to predate on eggs and chicks (Maclean 1973b; Marsden 1999; Chapter 2). Another nest predator, although with markedly lower impact, is the pygmy falcon *Polierax semitorquatus*, which may remove chicks from inside the nest chambers (Covas et al, unpublished). Both snakes and pygmy falcons will normally take the whole brood (pers. obs.); I therefore assumed that if at least one nestling was present in the nest during a given visit, that nest had not suffered predation; a nest was considered depredated if it was found empty on a visit following a day when we found a snake foraging or feeding at that colony. If no snake was seen at the colony on a previous visit, but the contents of two or more adjacent nests disappeared suddenly, these were also considered to have been depredated.

Rainfall data was collected in the study area using a rain gauge.

Statistical methods

I manipulated a total of 63 broods. Due to high nest predation, the sample sizes decreased markedly during the nestling period and only 28 broods produced fledged young (12 controls, 11 enlarged and 5 reduced). Therefore the sample sizes vary for different analyses.

Sociable weavers made several breeding attempts in both seasons and most individuals were present in the area in both years of the study. To guarantee independence of data only one manipulation was conducted for any breeding pair. Yet, if the brood got depredated before day 6 that pair was reassigned to any treatment; this happened in only two instances.

Normally distributed variables (e.g. mass, number of chicks in the nest) were analysed using general linear modelling. Fledging mass was used as a measure of nestling condition since this seemed the index of body condition that best suited my data (see chapter 2). Variables with heterogeneous variances were log transformed. Proportion data (proportion of chicks present at days 9 and 17) were analysed

assuming a binomial distribution. All variables were analysed using GLIM 3.77. Modelling was begun with all factors and pertinent interactions. A final model was selected after sequentially dropping all non-significant terms, with the significance of terms being determined by the change in deviance after the term was dropped from the model. A post-hoc t-test was conducted to analyse which levels of the factor differed significantly. The following factors were considered in all models: rainfall, year and treatment. In preliminary analyses I also included 'group type' as a two-level factor (for nests attended by pairs alone or pairs with helpers), but this factor was dropped from all analyses where it was not significant (i.e. all but one; see below). Rainfall was included as the total over the 30 days prior to the day when measuring and counting the chicks took place (see chapter 2 for more information on this criterion). I considered 2 categories of rainfall: '1'< 100mm, '2'≥ 100mm. These categories were chosen based on the results obtained on the effect of rainfall on reproductive effort and reproductive success (Chapter 2).

RESULTS

Feeding rate

Sociable weavers did not work harder to raise enlarged broods. The brood size manipulations affected the feeding rate significantly (main factor 'treatment': $F = 9.47$, d.f.= 2, 22, $p < 0.025$; Fig 5.1), but only reduced broods differed significantly from controls by receiving fewer feeding visits ($t = 2.79$, d.f.= 20, $p < 0.01$). There was no difference in the feeding rates between control and enlarged broods ($t = 0.44$, d.f.= 20, $p > 0.25$). There was, however, a tendency for experimentally enlarged broods attended by pairs with helpers to have a higher feeding rate, but this was not significant (interaction treatment*group type: $F = 3.33$, d.f.= 2, 16, $p = 0.07$).

Nestling mortality

Sociable weavers never raised a fully enlarged brood and in only three out of eleven nests did one extra chick fledge (i.e. in 27% of the enlarged nests). Deaths occurred

early in the nestling period: at day 9 (i.e. less then halfway through the nestling period) there was already a significant effect of treatment on nestling survival (χ^2= 18.12, d.f. =1, $p < 0.001$). As a result, the number of nestlings present in the nest at day 9 no longer differed significantly between control and enlarged broods (F= 1.12, d.f.= 1, 34, $p > 0.25$; Fig. 5.2). The same results were found at day 17, although the difference in mortality between controls and enlarged broods was less pronounced (χ^2= 3.88, d.f.= 1, $p < 0.05$), probably reflecting the fact that nestling mortality was also high in control broods. Enlarged broods did not fledge more chicks than control broods (number of chicks in the nest at day 17: F= 0.28, d.f.= 1, 22, $p > 0.5$). Factors 'rainfall' and 'year', and interactions 'rainfall*treatment' and 'year*treatment' were not significant.

Fledging mass

Treatment had no significant effect on fledging mass (F= 1.29, d.f.= 2, 18, $p > 0.25$; Fig. 5.3), nor did any of the other explanatory variables.

DISCUSSION

As expected, sociable weavers did not increase workloads to raise the enlarged broods, and never raised a fully enlarged brood. Chicks in enlarged broods had no significant differences in mass at fledging, which might suggest that weavers favoured quality to quantity.

The results presented here contrast with most brood size manipulations conducted in northern regions, where parents usually raise more young in enlarged broods, although chicks often fledge in lower condition than control broods (reviewed in VanderWerf 1992). Few brood size manipulations have been conducted at low latitudes. Poiani (1993) found that bell miners did not increase their feeding rates for enlarged broods. Fledging success in his study was generally low, but enlarged broods fledged more young than control broods. A three-year study on tropical house wrens (Young 1996) found that adults increased their workloads to

raise enlarged broods. However, parents successfully raised the enlarged broods in two years of the study when conditions were good, but not in a bad year. In contrast, tropical snail kites *Rostrhamus sociabilis* (Beissinger 1990) and white-rumped swiftlets *Aerodramus spodyopygius* (Tarburton 1987) did not raise enlarged broods. These studies are to some extent difficult to interpret since the authors do not provide adult survival estimates for the populations. Still, they seem to indicate that brood size manipulations at low latitudes do not result in a marked increase in reproductive effort or number of young fledged.

All parents are expected to produce a clutch that maximises their fitness. This includes not only the current brood, but also the parents' prospects of survival and future fecundity (Stearns 1992). Therefore parents faced with an artificially enlarged brood should make investment decisions in relation to their future reproduction prospects (which includes survival). They may choose not to work harder, or to only increase workloads to a certain level, if that compromises their future fitness. Sociable weavers enjoy relatively high survival (Chapter 3). They inhabit a variable environment, where reproductive success is generally low due to high nest predation and high variation in rainfall (Chapter 2). Still, breeding periods are usually elongated, with several nesting attempts, which is probably costly (Lindén & Møller 1989). Under these circumstances it seems advantageous to safeguard one's survival, to the detriment of one's offspring's since surviving to reproduce in a good season may significantly increase lifetime reproductive success (Stearns 1992; Charlesworth 1994; Erikstad *et al.* 1998). In contrast, species with low survival prospects could be expected to increase investment in current reproduction to some extent, even if there is some cost of parental survival (Charlesworth 1994), resulting in an increase in the number of young produced.

The role of food availability

The most common interpretation for failure of parents to raise an enlarged brood is to attribute it to food limitation (e.g. VanderWerf 1992). This interpretation might be wrong in many cases since brood size manipulations are adequate to examine the cost

of reproduction in birds (Lindén & Møller 1989; Erikstad *et al.* 1998) and cannot clearly distinguish between food limitation and unwillingness to work harder to raise the extra chicks (see also Martin 1995). Food availability at the time of manipulation is however expected to influence parental investment decisions. Erikstad *et al.* (1998) modelled the optimal balance between reproductive effort and adult survival for long lived birds breeding in variable environments. According to this model, during normal breeding conditions parents are expected not to work harder to raise an experimentally enlarged brood, but might increase their breeding effort when conditions are exceptionally good. This has been shown for a number of species (Johnsen *et al.* 1994; Erikstad *et al.* 1997; Erikstad *et al.* 1998). My study included an exceptional period when conditions were above average, but I only had the chance to perform three enlarged brood manipulations during that period. Of these, only one fledged one extra chick, so it does not seem that sociable weavers did increase substantially their breeding effort under good conditions, although that could only be ascertained with further study. Sociable weavers normally adjust the feeding rate to the number of chicks in the nest (Chapter 2). In this experiment, they decreased the feeding rate at reduced broods, but did not increase it to raise the enlarged broods. This suggests they were unwilling to increase current parental investment at the expenses of future reproduction, in agreement with what is predicted for long-lived birds in variable environments (Curio 1988; Woller *et al.* 1992; Charlesworth 1994).

Offspring quality

Fledglings produced in enlarged broods had no significant differences in mass at fledging. Given that sociable weavers did not increase feeding rates at enlarged nests, a decision had to be made about whether to distribute food equally among nestlings, thus fledging an enlarged brood of inferior condition, or whether to invest in fewer young of better condition. The result obtained suggests weavers might favour quality to quantity of young. This result should be interpreted with caution, due to the small sample size used in fledging mass analysis. Still, it is interesting as it reinforces the

differences in response to brood size manipulations at different latitudes, since in the north the young of enlarged broods generally fledge at lighter weights.

The offspring quality hypothesis has been suggested to explain some differences in life history characteristics of northern and southern birds, namely, differences in clutch size, duration of parental care and tolerance of offspring in the natal territory (Martin 1996; Young 1996; Martin *et al.* 2000). To produce good quality offspring in the south might be important if high survival in these areas generates increased competition for territories or mates (Martin 1996; Young 1996) or if increased investment in offspring translates into increased resistance against parasites (Ricklefs 1992). To my knowledge, the offspring-quality hypothesis remains untested.

DEDICATION

This paper is dedicated to the memory of Christer Hemborg, who motivated me to conduct brood size manipulations on sociable weavers, gave valuable help and advice when I started the fieldwork, and provided much needed encouragement to face the first snakes.

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FIGURES

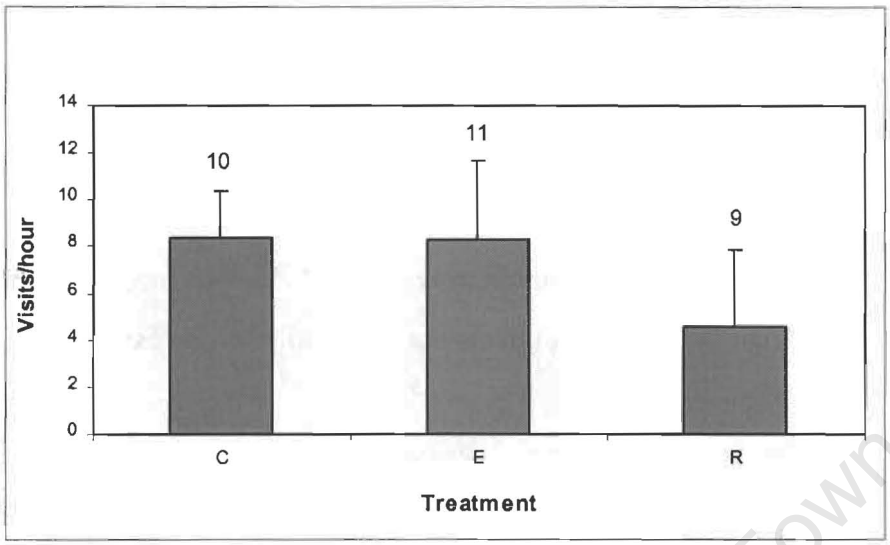

Fig. 5.1. Feeding rate (number of visits to the nest per hour) in enlarged, reduced and control broods. Bars represent mean and SE of data. Sample sizes are shown above the bars.

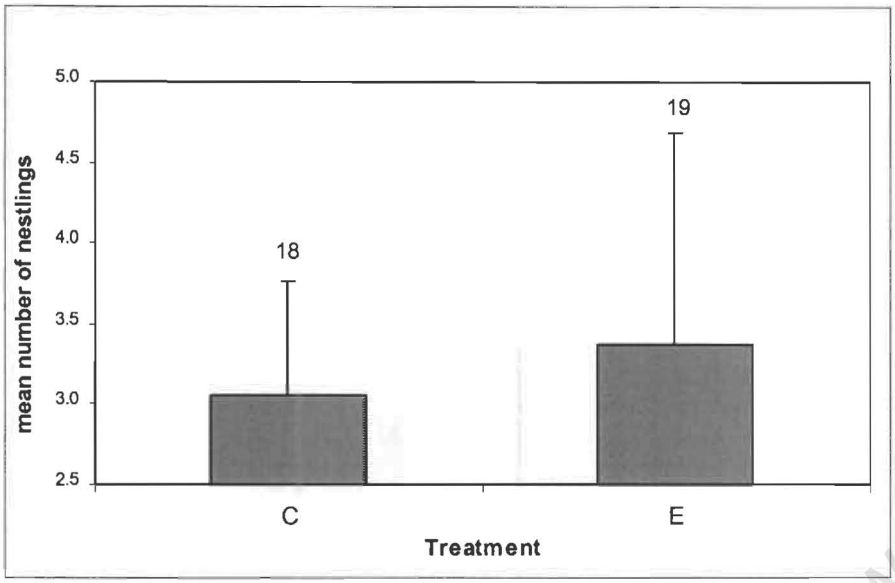

Fig. 5.2. Number of chicks present in the nest at day 9 in enlarged and control broods; the differences are not significant. Bars represent mean and SE of data. Sample sizes are shown above the bars.

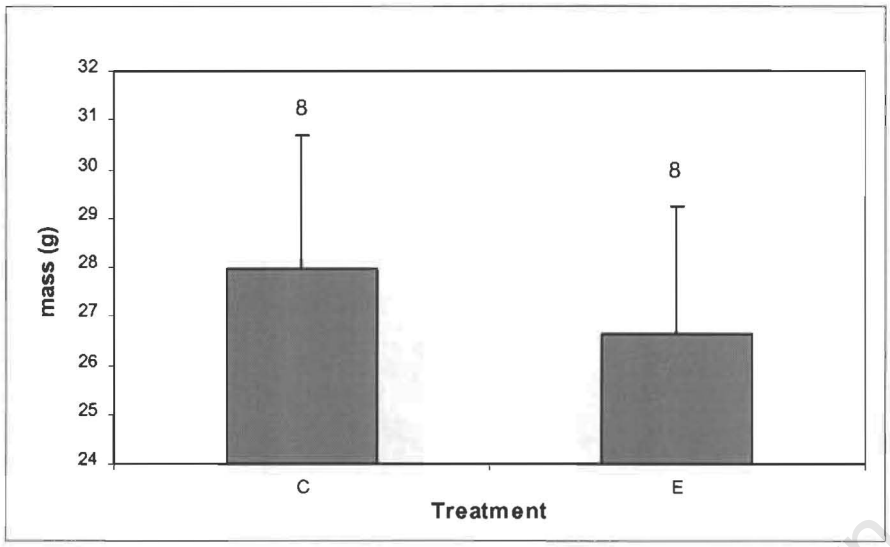

Fig. 5.3 Mass before fledging (day 17) in enlarged and control broods. The differences are not significant. Bars represent mean and SE of data. Sample sizes are shown above the bars.

6

Cost of reproduction and delayed breeding in a cooperative breeder: an experimental approach

In cooperatively-breeding birds some individuals forego independent breeding. This has usually been explained through the existence of ecological constraints on independent breeding, or through a combination of ecological constraints with benefits of remaining in the natal territory. Here, I take a different approach to this question by studying a colonial cooperative breeder with no apparent ecological constraints, and where individuals may breed in their natal colony. Therefore, individuals can breed independently without losing the benefits of remaining at home. I concentrate on the question 'why do some birds forgo reproduction?' Sociable weavers are relatively long lived and inhabit a fluctuating environment where reproductive success is low and varies between years. I hypothesised that in this species reproduction is delayed under sub-optimal conditions to delay the cost of reproduction and increase survival. Hence, I predicted that a reduction in the cost of reproduction in this species would result in an increased proportion of breeding birds and increased breeding activity of younger birds. I experimentally reduced the cost of reproduction through food supplementation at some colonies. As predicted, the experiment resulted in increased breeding activity and yearlings engaged in reproduction at colonies supplemented with food but not at control colonies. I suggest that a 'cost of reproduction' approach might be relevant to understand the link between life histories and cooperative breeding.

INTRODUCTION

Many animal species delay the onset of reproduction for one or more years and may forgo breeding in some years. This behaviour has attracted attention in many species, but is particularly relevant in group-living species since young that delay reproduction typically remain in the natal territory and may act as helpers-at-the-nest. Attempts at explaining delayed reproduction in cooperative breeders focused initially on ecological constraints, suggesting that opportunities for independent breeding were limited due to habitat saturation (Emlen 1982; Emlen 1991). For example, independent breeding could be limited by shortage of breeding territories or mates. However, some species still delay dispersal when suitable - but perhaps lower quality - habitat is available (Stacey & Ligon 1987; Macedo & Bianchi 1997; Ekman *et al.* 2001). This suggests that the fitness benefits of initiating breeding in poor territories might be lower than those obtained by staying at home (whether helping or not) while waiting for a more suitable breeding option (Stacey & Ligon 1987; Ekman *et al.* 2001). Implicit in this hypothesis is the assumption that reproduction has a cost that should only be incurred when the benefits are sufficient to compensate for it in terms of lifetime fitness. This view is particularly relevant for relatively long-lived species with low fecundity such as most cooperative breeders (Arnold & Owens 1998). In species with these life history traits even a small reduction in survival can have significant effects in terms of lifetime fitness (Williams 1966; Curio 1988; Charlesworth 1994). Yet, an experimental link between breeding conditions, cost of reproduction and the decision of becoming a breeder has not been established in cooperatively-breeding species.

Several studies on group-living birds have examined the decision of dispersing to breed versus delaying dispersal and showed that individuals have a preference for high quality territories, often delaying reproduction if these are not available (e.g. Stacey & Ligon 1987; Komdeur *et al.* 1995; Ekman *et al.* 2001). These studies are revealing, but have two limitations. First, territory quality was inferred and not manipulated. Second, in these species young usually need to disperse to acquire breeding status, and therefore the cost of breeding is also associated with losing important benefits of

staying at home, such as enhanced survival (e.g. Ekman *et al.* 1999; Green & Cockburn 2001). A non-territorial colonial species where breeding status can be acquired at the natal colony could avoid these limitations. In other words, in such a species, the dichotomy 'benefits of philopatry' versus direct fitness benefits of independent breeding would not apply. This would allow one to concentrate on the question 'why do some birds forgo independent breeding' without having to control for possible benefits of group size or remaining at home.

The sociable weaver *Philetairus socius*, is a relatively long-lived (up 9+ years; *ca* 66% annual survival; Chapter 3) colonial cooperatively-breeding passerine. These birds inhabit a very large thatched nest mass built communally by the whole colony throughout the year. Young sociable weavers only seldom engage in reproduction in the first two years of life and will commonly remain with the parents as helpers-at-the-nest, although most colonies also have a variable percentage of floaters. Contrary to many other cooperatively breeding systems, delayed reproduction in the sociable weavers cannot be explained by a shortage of breeding territories. Dispersal in this colonial bird is low (only 6% of the birds ringed over 8 years were recaptured at other colonies), and birds frequently become breeders in their natal colony (over 60%; Chapter 2). Shortage of mates does not seem to be a limiting factor either, since the sex ratio in the population is approximately even (Doutrelant & Covas, in prep.). Moreover, delayed reproduction amongst birds of up to two years is equally common in males and females. Since sociable weavers often become breeders at their natal colony, the acquisition of breeding status in this species is not necessarily associated with loss of benefits of staying at home.

I hypothesised that sociable weavers forego reproduction when young to delay the cost of reproduction. Similarly, older individuals in the population should balance breeding conditions in relation to the prospects of breeding output to decide whether or not to engage in breeding activity. Consequently, the proportion of breeders should vary according to the cost of reproduction.

In this study I experimentally reduced the cost of reproduction at some colonies by reducing reproductive effort and other potential costs associated with food

acquisition (such as predation risk and travelling time) through an easily obtainable food supplement. I predicted that food supplemented colonies should differ from controls in having: 1) higher percentage of birds breeding; 2) fewer helpers at each nest, or lower percentage of nests with helpers, as potential helpers would engage in independent reproduction; and 3) lower average age of breeders, or increased proportion of 1-2 year-olds breeding.

METHODS

Study area and species

The sociable weaver is a 26-32 g passerine endemic to the arid and semi-arid savannahs of south-west Africa. These weavers are sedentary, and build a large communal nest mass that is occupied by the whole colony year-round. In each colony a variable number of individual nest chambers will be used for breeding in. Those same chambers are used by the breeding pair, their helpers and offspring to roost in. Sociable weavers are facultative cooperative breeders, and between 40-80% of the breeding pairs are assisted by helpers (Chapter 2). Helpers are usually young from earlier broods, but unrelated birds may also help (Chapter 2).

Sociable weavers feed on insects, seed and other plant products, foraging predominantly on the ground, but also on the bark and leaves of trees (Maclean 1973b). Their food supply, as in most arid region birds, is strongly influenced by rainfall (Maclean 1970; Maclean 1973b; Lloyd 1998), which explains most of the variation in reproductive parameters and, for successful broods, reproductive output (Chapter 2, Maclean 1973a; Marsden 1999).

The experimental component of this study was conducted during two breeding seasons, between Sep. 1999 – Apr. 2000 and Sep. 2000 – Jan. 2001. The study took place at Benfontein Game Farm near Kimberley in the Northern Cape province, South Africa. The vegetation in the study site consists of open *Acacia* savannah dominated by *Stipagrostis* grass. The study area contains 24 sociable weaver colonies, each comprising between 10 and 200 birds. The birds in 15-20 of these colonies have

been regularly captured and ringed twice a year since 1993, as part of an ongoing study. Thus birds' age and colony of origin was known in many cases. I started ringing chicks in the nest in 1998, and all individuals were ringed with a unique colour combination.

Experimental design

For the experiment presented here, I used 8 colonies as treatments (food supplemented), ranging in size from 20-60 individuals, and 10 as controls, ranging from 20-120 individuals. The colonies were assigned randomly as treatments and controls. In 2000, the birds were captured at these colonies with mistnets in the beginning of the breeding season. Some birds could escape by flying over the nets, but capture success was usually above 80%. The birds that escaped were counted and added to the total captured, producing a reliable estimate of colony size.

All colonies were visited every 4-7 days, and the nest contents were inspected for the initiation of new clutches. A hide was placed 2-5 m away from the colony to conduct 2-6 h observations (on different days), in order to identify the colour rings of all the individuals attending a given nest. These observations were also aimed at identifying immigrants that had moved into the colony.

Food-supplemented colonies were provided with a daily portion of seed (a mixture of canary seed, mixed millet and red rape) throughout the breeding season. Depending on the colony size, these colonies were fed early every morning with 0.5-1.5 kg of seed. The seed was scattered on the ground under the colonies or up to a maximum of 2 meters from it. The food was readily taken by the birds.

Statistical methods

Proportion data (nests with helpers per colony and proportions of birds breeding) were analysed assuming a binomial distribution. Proportion of birds breeding was defined as the maximum number of birds breeding in a colony in a given year divided by the total number of birds present in that colony during that breeding season. Mean group size (number of birds attending a nest), a continuous variable, was analysed

using general linear modelling. All analyses were done using GLIM 3.77. In case of binomial error, the dependent variable was number of birds breeding or the number of nests with helpers, and the binomial denominator was the total number of birds present in the colony or the total number of nests. Modelling began with a full model, and a final model was selected after sequentially dropping of all non-significant terms. The significance of terms was determined by the change in deviance after the term was dropped from the model. The factors included in the analyses as categorical variables were treatment (control or food supplemented), year, and colony size ('small' < 40 individuals; 'big'> 40 individuals). Colony size categories were decided based on preliminary analyses that showed differences in reproductive parameters (e.g. hatching success and fledging mass) between colonies grouped according to these categories.

RESULTS

Food supplementation resulted in a significant increase in the proportion of birds breeding (χ^2= 9.85, d.f.= 17, p< 0.005; Fig. 6.1). There was a tendency for the addition of food to have a stronger effect on the proportion of birds breeding in smaller colonies, but this was not significant (interaction of treatment with colony size χ^2= 3.14, d.f.= 14, p= 0.08). Factors 'year', 'colony size' and the interaction of 'treatment' with 'year' were non-significant.

The increased proportion of breeding birds was not due to immigration, since I only recorded two birds moving into a treatment colony after food supplementation started, and four birds moved into one of the control colonies.

The average group size (i.e. number of birds tending a nest) decreased significantly in food supplemented colonies (F= 8.67, d.f.= 1,12, p< 0.025; Fig. 6.2). However, it varied significantly between years, with larger groups in 2000 (F= 24.4, d.f.= 1,12, p< 0.001). The interaction between treatment and year was also significant (F= 4.96, d.f.= 1.10, p< 0.025; Fig. 6.3), showing a stronger effect of food supplementation in 2000. The proportion of nests with helpers also varied significantly between years, being higher in 2000 (χ^2= 5.528, d.f.= 1, p< 0.025). The

experiment had no significant effect on the proportion of nests with helpers within each colony.

In both control and food supplemented colonies between 20-30% of individuals were of undetermined age that had been ringed as adults between 1998-2000. Also in both treatments, reproduction remained dominated by breeders that were 4-9 years old (70-80%). Yet, in food supplemented colonies I recorded four first year old birds breeding. This was in sharp contrast with control colonies, where no yearlings were recorded to have attempted to breed.

DISCUSSION

The food supplementation experiment caused a clear increase in the proportion of birds breeding. This result was not due to increased immigration, since I did not record any more immigrants moving into food supplemented colonies than I did into controls. The experiment also caused a decrease of the age of first reproduction, as four yearlings bred in food supplemented colonies while no yearlings attempted to breed in control colonies. There was a decrease in the number of helpers per nest in food supplemented colonies, suggesting that part of the extra breeders in these colonies would normally have acted as helpers instead of engaging in independent reproduction. The treatment had a stronger effect in 2000, which is likely due to the lower proportion of nests with helpers in the population in 1999 (30%, with generally only one helper per nest) than in 2000 (80%, with up to 5 helpers per nest; Chapter 2). However, these results should be interpreted with caution because only two food supplemented colonies could be included in the analyses of group size in 2000 (i.e. 10 groups), since high nest predation at another colony prevented a confident identification of the composition of enough groups.

At a proximate level, the decision of whether or not to breed in the sociable weaver seems to be influenced by food levels. Under natural conditions more individuals engage in reproduction in good rainfall years and breeding effort increases compared to low rainfall years (see Chapter 2). However, even during an above

average rainfall year such as 1999 there were no yearlings breeding in control colonies, suggesting that food abundance alone does not explain why many birds forego reproduction.

To reproduce, parents must acquire additional food. Even if food is abundant, the morphology and physiology of organisms limit food acquisition, which places a cost on reproduction (Stearns 1992). In addition, in order to forage for themselves or to feed their offspring, parents spend time and energy and incur predation risks. In fact, in birds reproduction has been experimentally shown to decrease survival of breeders (e.g. Visser & Lessels 2001), confirming that the cost of reproduction is a central concept in life history theory (e.g. Bell 1980, Stearns 1992, Charlesworth 1994). If reproduction has a cost that will reduced future fecundity or survival, than potential breeders must balance these costs against the fitness benefits of engaging in breeding activity. In this experiment I provided additional food that could be obtained at a negligible energetic cost and predation risk to adults, since it was placed under the nest. This clearly would have reduced the time spent and risks incurred to obtain food, thus decreasing the overall costs of reproduction associated with foraging. An increase in numbers of birds breeding in response to this manipulation indicates that the variation in breeding conditions and associated cost of reproduction clearly influence the decision of whether or not to breed independently.

The fact that in many species individuals do not breed in any given year, even though they are capable of doing so, has for long posed a challenge to biologists. Recently, evidence has been accumulating that there can be strong fitness benefits of delaying dispersal, remaining in the natal territory and associating with parents (Ekman *et al.* 1999; Green & Cockburn 2001), even without considering the potential benefits of helping-at-the-nest. Most cooperative breeders are group-territorial and to obtain breeding status individuals require a territory. The decision of staying in the natal territory or dispersing to breed has been described by scientist as a threshold model that takes into consideration the costs and benefits of staying in the natal territory versus the options available for dispersing (Koenig *et al.* 1992). However, the biology of a number of species is such that they do not need to disperse or to inherit a

territory to acquire breeding status. This seems the case with most colonial (cooperative) breeders such as sociable weavers or white-fronted bee-eaters *Merops bullockoides* (Emlen 1990). Delayed reproduction could be selected as a life history strategy if earlier maturation reduces future survival or fecundity (Bell 1980; Stearns 1992), for example, if young are less efficient at foraging or are worse competitors and will therefore incur a disproportionately high cost of reproduction. The argument is equally valid for 'sabatical years' taken by mature adults that could have bred previously: when conditions are such that reproduction will incur a considerable cost it might be advantageous to delay reproduction until conditions improve. In fact, the proportion of sociable weavers breeding varies greatly within and between years (see Chapter 2) and there is also evidence of whole populations skipping breeding in unusually bad years (Maclean 1973a; Chapter 3). Investing in survival should be particularly important in variable environments where reproductive success varies greatly between years, as is the case for this species due to high variability in rainfall and high nest predation (see Chapter 2). A longer life span will allow a greater number of breeding events, increasing the possibility of breeding in a good year, thus considerably increasing lifetime reproductive success (Stearns 1992; Erikstad *et al.* 1998; Chapter 2). In contrast, species with low survival prospects will often not live to breed again, so they are expected to maximise investment in current reproduction, even at the expense of survival (Charlesworth 1994).

Life histories and cooperative breeding

Understanding why grown offspring delay dispersal (and reproduction) is the key to understanding the evolution of cooperative breeding (Emlen 1991; Hatchwell & Komdeur 2000). A 'cost of reproduction' approach to the study of cooperative breeding might be relevant. Recently Arnold & Owens (1998) showed that cooperative breeding is more prevalent in species with high survival and low fecundity. They proposed that the link between this life history pattern and cooperative breeding was a lower territory turnover resulting from longer occupation of territories by long-lived individuals. This would create habitat saturation that

would limit opportunities of breeding independently, which would lead young to delay dispersal and, eventually, to engage in helping. Therefore, the proximate mechanism suggested by these authors is an 'ecological constraints' mechanism. While I acknowledge that physical habitat is limiting in many cases, I believe that this explanation does not apply to all species. I suggest that the study of delayed maturity and cost of reproduction may provide important insights to our understanding of the link between life histories and cooperative breeding.

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FIGURES

Fig. 6.1. Proportion of birds breeding in control and food supplemented colonies. Small squares denote means, boxes denote standard errors, and vertical lines denote standard deviation.

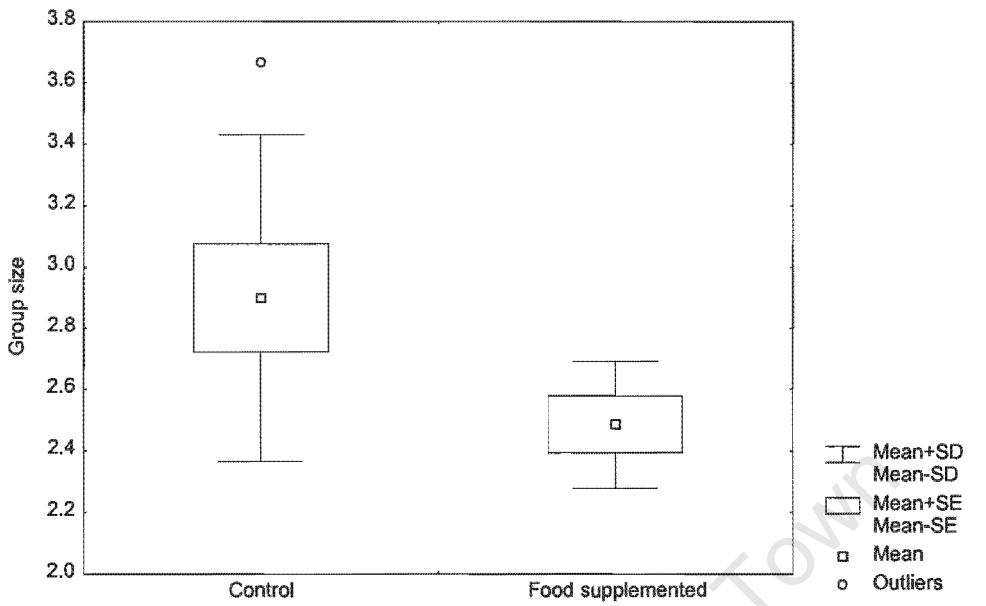

Fig. 6.2. Average group size (number of birds attending a nest) in control and food supplemented colonies. Small squares denote means, boxes denote standard errors, and vertical lines denote standard deviation. The circle is an outlier.

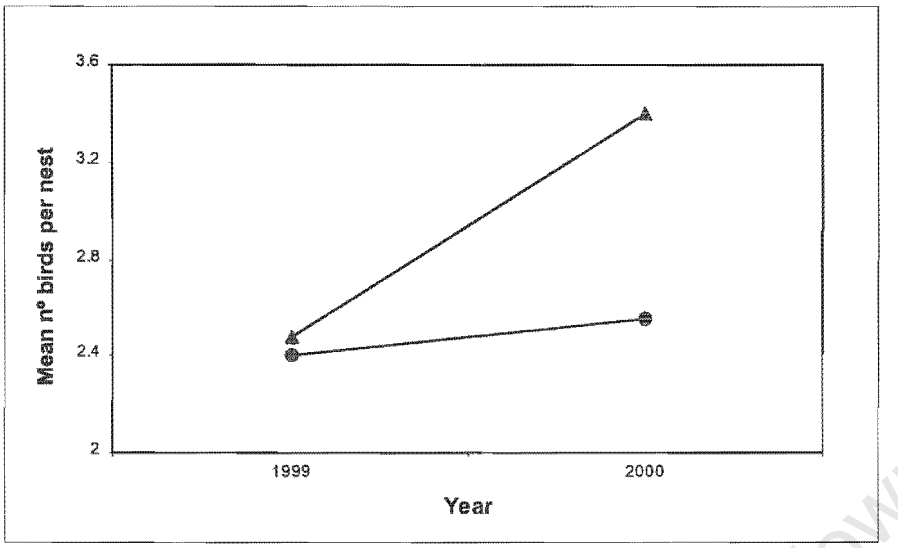

Fig. 6.3. Average group size in control (▲) and food supplemented (●) colonies in 1999 and 2000. See text for statistical interpretation of this result.

7

Synthesis

LIFE HISTORY PATTERN AND EVOLUTIONARY HYPOTHESES

Sociable weavers life history characteristics proved typical of 'southern' passerines in being typified by small clutches, multiple broods, extended parental care, extended occupation of the parental territory, and high juvenile and adult survival (Chapters 2 and 3). The latitudinal pattern in avian life histories has been attributed to several hypotheses related to food limitation, nest predation and reduced seasonality leading to increased survival. An understanding of the role played by the different factors in shaping life histories at low latitudes has been hindered by the lack of detailed studies from these regions. In this study I used correlative methods, capture-recapture techniques and experiments with the aim of understanding the role of different environmental factors and trade-offs in shaping the life history of the sociable weaver. The main results of this thesis and their implications are discussed below.

Food availability vs. survival

Food availability (measured here as rainfall) played a major role in determining reproductive effort and reproductive success of sociable weavers (Chapter 2). In good rainfall years the breeding season lasted considerably longer and clutch size, fledging success and fledgling mass increased significantly after good rains. The effect of food

limitation on avian reproductive effort is well documented and variation in food levels can explain a substantial part of the within-species variation in avian life histories (reviewed in Martin 1987). If the observed reduction in reproductive effort translates into a substantial decrease in mortality, and if there is a consistent latitudinal decrease in food availability, then food could explain the geographical pattern in life histories. It has been suggested that tropical and southern temperate regions have lower food productivity because reduced seasonality and greater diversity of prey make food acquisition more difficult (reviewed in Martin 1996). However, in a field experiment study comparative South and North America Martin *et al.* (2000) showed that more food was brought to each nestling in a site in Argentina (where clutches were smaller) than in Arizona, suggesting it is doubtful whether food is generally more limiting in the south. In this study I found that sociable weavers always made several breeding attempts per season (even in bad years). The fact that individuals may remain in breeding condition for several months seems contrary to the food limitation hypothesis (Martin 1996). Still, this result might be due to the seasonal pattern of resources rather than to total food abundance. If the seasonal increment in resources for breeding lasts several months, but has reduced amplitude, this could make it advantageous to lay several small clutches instead of one large clutch.

Also not clear is to what extent reduced reproductive effort may result in increased survival. Sociable weavers had high survival compared to most similar size European passerines (i.e. 0.66 compared to approximately 0.5; see Sæther 1989). The survival analyses presented in Chapter 3 showed no time-dependence, i.e. there was no significant variation in survival between years. Yet, reproductive effort varied substantially between the years included in the analyses (i.e. from one year during which no breeding activity was detected to a 9-month breeding period). Of course, a problem with correlative studies such as this one is that reproductive effort might be adjusted to environmental conditions, making variations in survival difficult to detect. Still this result does not support the hypothesis that high survival is achieved through reduced reproductive effort. Furthermore, the high juvenile and adult survival obtained, and a lack of effect of rainfall (as a measure of food availability) is difficult to

reconcile with food limitation and suggest that extrinsic factors promoting high survival could play an important role.

Recently, it has been suggested that latitudinal differences in avian life histories could be caused by differences in extrinsic mortality rates (Martin 2002). Birds in the north would face harsher winters, which would yield increased mortality, whereas milder winters in the south would promote reduced mortality. According to life history theory, an increase in adult survival should favour reduced reproductive effort (Murphy 1968; Stearns 1992; Charlesworth 1994). In relatively long-lived species a small reduction in survival could substantially decrease lifetime reproductive success (Williams 1966; Curio 1988; Charlesworth 1994), thus breeders in southern regions should be less willing to risk their survival in relation to that of their young (Ghalambor & Martin 2001; Martin 2002).

The results of two experiments conducted here seemed to indicate that favouring survival to increased investment in reproduction is an important characteristic of sociable weavers' life history. In agreement with the extrinsic survival hypothesis, sociable weavers did not work harder to raise an artificially enlarged brood. This resulted in increased fledging mortality, but there were no differences in fledgling mass (Chapter 5). Also in line with the extrinsic survival hypothesis, the number of birds that engaged in breeding increased significantly when the cost of reproduction was decreased through a food supplementation experiment (Chapter 6). This result was probably due to a decrease in the cost of reproduction and not directly related to food limitation since yearlings engaged in breeding at food supplemented colonies but not at controls, even when natural food availability was high. Furthermore, the food given was of relatively poor quality compared to the natural situation (i.e. an artificial supplement of seed only, compared to a substantial increase in insects abundance after good rains), but was offered to the birds at virtually no cost of food finding.

Nest predation

Nest predation in this study was very high, with an average 70% of clutches laid being depredated (Chapter 2). According to life history theory, high juvenile mortality can lead to reduced fecundity and select for longer life in order to maximise the number of breeding events (Stearns 1992; Charlesworth 1994). Nest predation has in fact been shown to explain variation in avian life history traits (Cody 1966; Martin 1995; Martin & Clobert 1996), including an increase in survival (McCleery *et al.* 1996). The small clutches and relatively high survival found here are consistent with the nest predation hypothesis, although it is less clear why long developmental periods would have evolved under high nest predation. At a broader level, it is also not clear why nest predation should increase with latitude, and the evidence available does not confirm that is does. Studies at different latitudes have found predation rates that are inconsistent with a latitudinal pattern (see review in Martin 1996). The nest predation hypothesis was rejected in a recent study comparing bird communities in South and North America. Contrary to the prediction, Martin *et al.* (2000) found that nest predation rates were in fact lower, and clutches smaller in Argentina than in Arizona. Still, nest predation seems to be high in numerous southern African species. Crude information available on 51 *Brachystegia* woodland species gives a median of 71% eggs lost to predation (Vernon 1984). Another study from the arid south-western Africa also reported considerably high predation rates (e.g., larlike bunting *Emberiza imbetuani* 96%, rufouseared warbler *Malcorus pectoralis* 51%, chat flycatcher *Malaenornis infuscatus* 65%, Cape sparrow *Passer capensis* 80%; Lloyd 1998). The fact that the latitudinal pattern in avian life histories is clearly a global pattern suggests that a single explanation would account for it a global level. The nest predation hypothesis was rejected as responsible for the latitudinal pattern in South America, which could indicate that it might not play that major role. However, the high predation rates found in this and other studies of southern African birds suggest the study of nest predation in this region should be taken further.

Could environmental unpredictability play a role?

This study revealed that although sociable weaver reproductive success is generally low, it is highly variable. Individuals that breed in a year of good rainfall, or those who do not have their broods depredated, may experience a marked increase in their reproductive output.

Variation in reproductive success of a passerine is certainly not new. However, the magnitude of this variation in sociable weavers is noteworthy. Unpredictability of environmental conditions causing variation in reproductive success might be an important agent of life history evolutionary change (Stearns 1992; Charlesworth 1994). According to life history theory unpredictable mortality of young (i.e. nestlings) can select for an increased reproductive life-span, delayed maturation, reduced fecundity and increased phenotypic plasticity (Schaffer 1974; Schultz 1991; Stearns 1992; Charlesworth 1994). Therefore environmental unpredictability could in theory explain the life history strategy found in this study.

Rainfall-mediated environmental unpredictability seems to be an important characteristic of southern African ecosystems. Previous studies have reported the importance of rainfall in determining several breeding parameters of birds in southern Africa (e.g. onset of the breeding season, Maclean 1970; clutch size, Kemp & Kemp 1972; Lloyd 1999). Environmental unpredictability may also play an important role at a broader geographical scale. Many tropical and Southern Hemisphere regions are strongly affected by the El Niño Southern Oscillation (ENSO) (Allan *et al.* 1996). ENSO-induced changes in patterns of air circulation in the tropics bring about periodic El Niño and La Niña events, which cause negative and positive rainfall anomalies in these regions (Allan *et al.* 1996; Stone *et al.* 1996). By contrast, the Nearctic and Palearctic regions fall into convergent climate zones and are highly seasonal. ENSO is not associated with widespread negative anomalies in these zones, and hence rainfall is more predictable than in ENSO-affected regions (Stone *et al.* 1996). Thus, environmental unpredictability could contribute to explain differences in avian life histories between northern and southern latitudes. Several hypotheses have been put forward to explain the latitudinal pattern in avian life histories, but to my

knowledge, environmental unpredictability (or environmental fluctuation) has only been suggested in one study (Young 1996) and has not yet been investigated.

DELAYED DISPERSAL AND COOPERATIVE BREEDING

The study of cooperative breeding is guided by a widely accepted framework involving dissociation of two questions: 1) why do some birds forgo dispersal and independent reproduction and 2) why do these individuals help raising the offspring of other birds. The search for adaptive explanations for helping has resulted in a long list of hypotheses (reviewed in Cockburn 1998). This question was only marginally addressed in this thesis. There is weak evidence that sociable weavers might adjust helping behaviour under some circumstances (see Chapters 2 and 5). Such flexibility could be important in showing an adaptive character of helping behaviour (see Cockburn 1998). However, further study is necessary in this regard, as this topic fell outside the scope of this study. Instead, I was mainly interested in understanding why reproduction is delayed in the sociable weaver. The widely accepted answer to why individuals delay reproduction in cooperatively breeding species is that those individuals cannot breed elsewhere because of a shortage of breeding opportunities (the 'ecological constraints' or 'habitat saturation' hypothesis; see e.g. Gaston 1978; Emlen 1982; Brown 1987; Emlen 1991; Koenig *et al.* 1992). Why then should breeding opportunities be more limited for some species than other? The most common explanation is that there are peculiar features of these species' breeding ecology that make them more susceptible to habitat saturation (e.g. Emlen 1982; Koenig & Mumme 1987; Koenig *et al.* 1992). For example some cooperative breeders are cavity-nesters, and a shortage of cavities could prevent independent breeding (see references in Stacey & Koenig 1990). However, it has proven remarkably difficult to find common ecological correlates of cooperative breeding in birds (e.g. Ford *et al.* 1988; Smith 1990; du Plessis *et al.* 1995). Alternatively, it has been suggested that variation in life history traits could be a better predictor of cooperative breeding behaviour across species than ecological characteristics (the 'life history hypothesis'; Russell

1989). This hypothesis was recently analysed by Arnold & Owens (1998) who found a negative relationship between mortality and fecundity and the occurrence of cooperative breeding. They also found that more cooperative species occurred at low latitudes, in agreement with the latitudinal pattern in life histories. These authors suggest that high survival causes long occupancy of territories, leading to a low turnover of territories and hence reduced breeding opportunities. Therefore, at a proximate level, the mechanism suggested by these authors is habitat saturation, but this saturation is due to specific life histories and not to ecological factors. However, some birds still delay dispersal in the presence of suitable but sub-optimal habitat. Koenig *et al.* (1992) suggested this is likely to happen because there are also benefits of remaining in the natal territory. Therefore, the decision of staying in the natal territory or dispersing to breed would be best seen as a threshold model that considers the cost and benefits of both strategies. Although this model was a significant contribution to understand the role of habitat quality in delayed dispersal, it still does not explain why delayed dispersal is not also common amongst short-lived species with high fecundity that also experience habitat saturation.

More recently, it was suggested that delayed dispersal in long-lived species could be explained by parental nepotism (Ekman *et al.* 2001a). According to theoretical models, parents with good survival prospects may afford to concede resources to their grown offspring (Ekman & Rosander 1992; McNamara *et al.* 1996) which could increase juvenile survival and give the offspring an incentive to remain in the natal territory. This has been corroborated by field observations (Ekman *et al.* 1994; Ekman *et al.* 2000). The parental nepotism hypothesis is an important advance in that it provides an explanation for the life history correlates of delayed dispersal, dissociates delayed dispersal from 'ecological constraints' and is able to explain dispersal in saturated environments (Ekman *et al.* 2001a). Yet, it still does not account for postponed reproduction in species that do not need to acquire a territory to breed. For example, white-fronted bee-eaters *Merops bullockoides* are colonial, do not inhabit all-purpose territories, and their feeding 'territories' are not in short supply, yet cooperative breeding is common (Emlen 1990). Like the white-fronted bee-eater, the

sociable weaver is a colonial cooperative breeder with no apparent constraints on independent breeding. Yet, reproduction in the first two years of life is rare and many older birds do not breed regularly. Why should sociable weavers forgo reproduction?

The role of life histories revisited

Sociable weavers seemed to pursue a life history strategy where adult survival plays an important role in maximising lifetime reproductive success. This life history strategy is probably characteristic of other cooperative breeders, since they tend to be long-lived (Arnold & Owens 1998). According to the extrinsic mortality hypothesis (Martin 2002), adults with high survival prospects should be reluctant in trading off their survival against an increased investment in reproduction. Emlen (1990) suggested that the most important factor limiting breeding attempts in the white-fronted bee-eater was the high cost of breeding under certain conditions. In harsh seasons the costs associated with reproduction increase and constraints first affect the young or sub-ordinate individuals (Emlen 1990). An unfavourable benefit to cost of reproduction ratio probably explains postponed reproduction in sociable weavers. In the experiment described in Chapter 6, I manipulated the cost of reproduction through providing extra food at low cost in some colonies. This resulted in significantly increased breeding activity and yearlings engaged in breeding at food supplemented, but not at control colonies.

In long-lived species such as most cooperative breeders, lifetime reproductive success is probably maximised through the number of breeding events in life (Clutton-Brock 1988; Stearns 1992). Therefore, these species should refrain from breeding in marginal conditions, when success is probably low, since even a small decrease in survival could significantly affect life-time reproductive success (Williams 1966; Curio 1988; Charlesworth 1994). This could also explain the often-reported result of delayed dispersal even in the presence of suitable, but low quality, habitat (e.g. Komdeur 1992; Macedo & Bianchi 1997; Ekman *et al.* 2001b). If successful breeding in low quality areas can only be achieved at a prohibitively high cost, it would clearly be more advantageous to remain in the natal territory since this can significantly increase

juvenile survival (Ekman *et al.* 1999; Green & Cockburn 2001) and lifetime reproductive success (Ekman *et al.* 1999). In contrast, in short-lived species the probability of surviving to future reproduction is often so low that an increase in current reproduction at the expense of parental survival would be expected (Charlesworth 1994). I therefore suggest that understanding life-history strategies and the role of the cost of reproduction for different species might provide an important avenue for understanding the geographical and life-history correlates of cooperative breeding.

CONCLUSIONS

Understanding why species differ in their life history traits is a central question of life history theory. In birds, the main focus of life history studies has been on understanding variation in clutch size. This study has shown that focusing on clutch size might not be sufficient to understand variation in life histories across latitudes. Clutch size varied in response to food levels in sociable weavers, but this did not explain the relatively high survival in this species. Instead, I suggest that the life history pattern found here is perhaps best explained by relatively mild winters that favour reduced mortality. This in turn leads to a reduction in reproductive effort. However, in all likelihood other factors also play a role. As shown here, food availability influences breeding decision, but I suggest this is a proximate factor and not the ultimate factor causing the evolution of this life history strategy characterised by enhanced survival, reduced fecundity and increased investment in parental care. The role of nest predation and variation in food levels between years (leading to variation of reproductive output) should be further investigated. Theoretical and empirical studies have shown that increased mortality of young (i.e. nest predation) and environmental unpredictability might play an important role in driving life history evolution. The predictions made by both models overlap and I did not try to separate them in this study. However, the results found here suggest they might play a role.

Therefore, I propose that the life history pattern of the sociable weaver might be seen according to the model depicted in Figure 7.1. In short, survival is favoured by relatively mild winters, which favours reduced reproductive effort and delays the onset of breeding. Variation in food levels within and between years, and high nest predation create uncertainty of breeding output, which should further favour investment in survival and reduced fecundity. Finally, at a proximate level, food availability influences clutch size and the decision of whether or not to breed independently.

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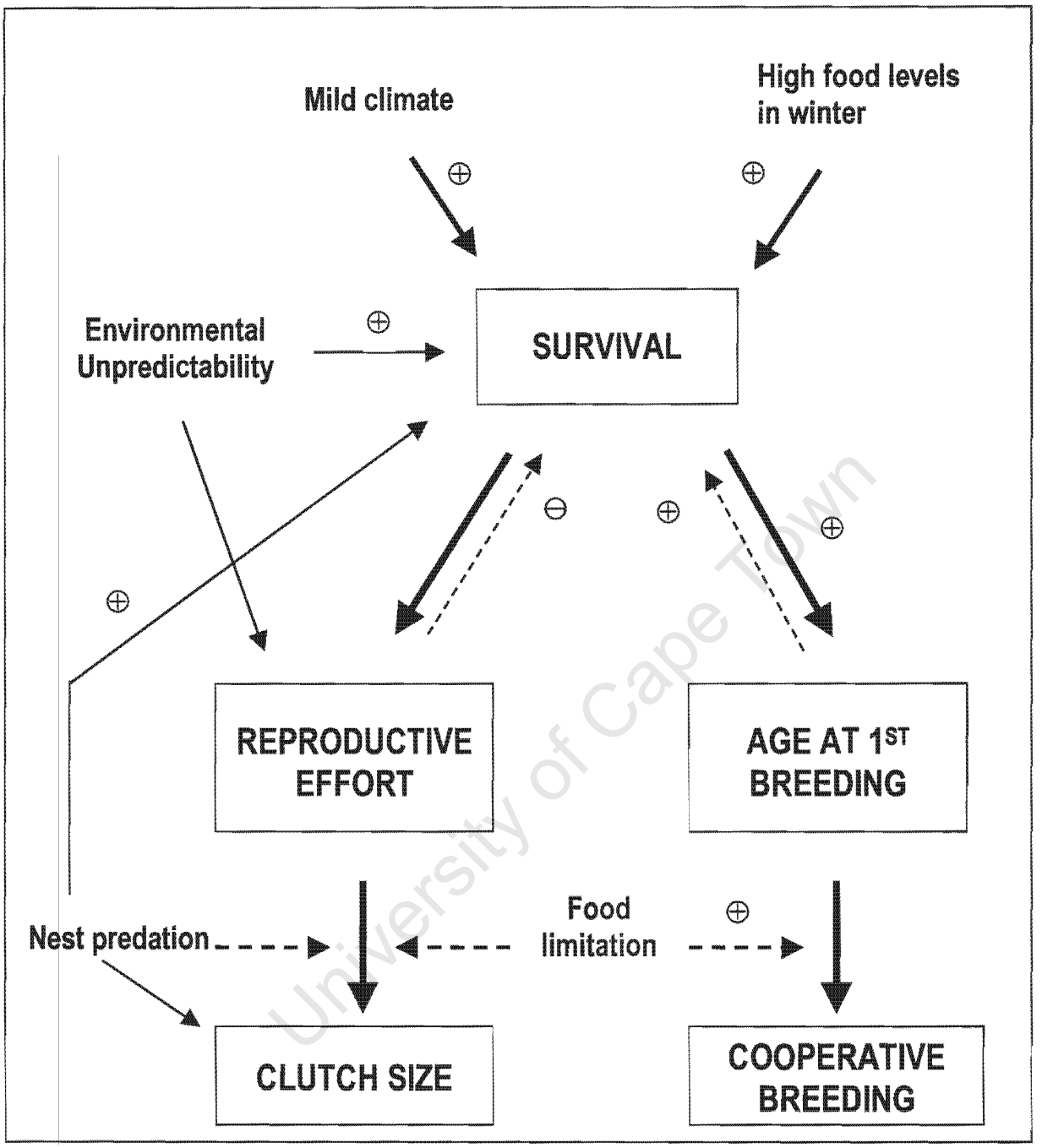

Fig. 7.1. Simplified and schematic view of the main factors influencing the evolution of the life history strategy of sociable weavers. Symbols ⊕ and ⊖ indicate positive or negative relationships. Arrows indicate evolutionary factors. Thick arrows represent main effects and thin arrows indicate secondary effects. Dashed arrows represent proximate factors. Benign winters favour reduced mortality leading to reduced reproductive effort and delayed onset of breeding, creating conditions for cooperative breeding to occur. Variation in food levels and nest predation create uncertainty of breeding output, which should further favour high survival and reduced fecundity. At a proximate level, food availability influences clutch size and the decision of whether or not to breed.